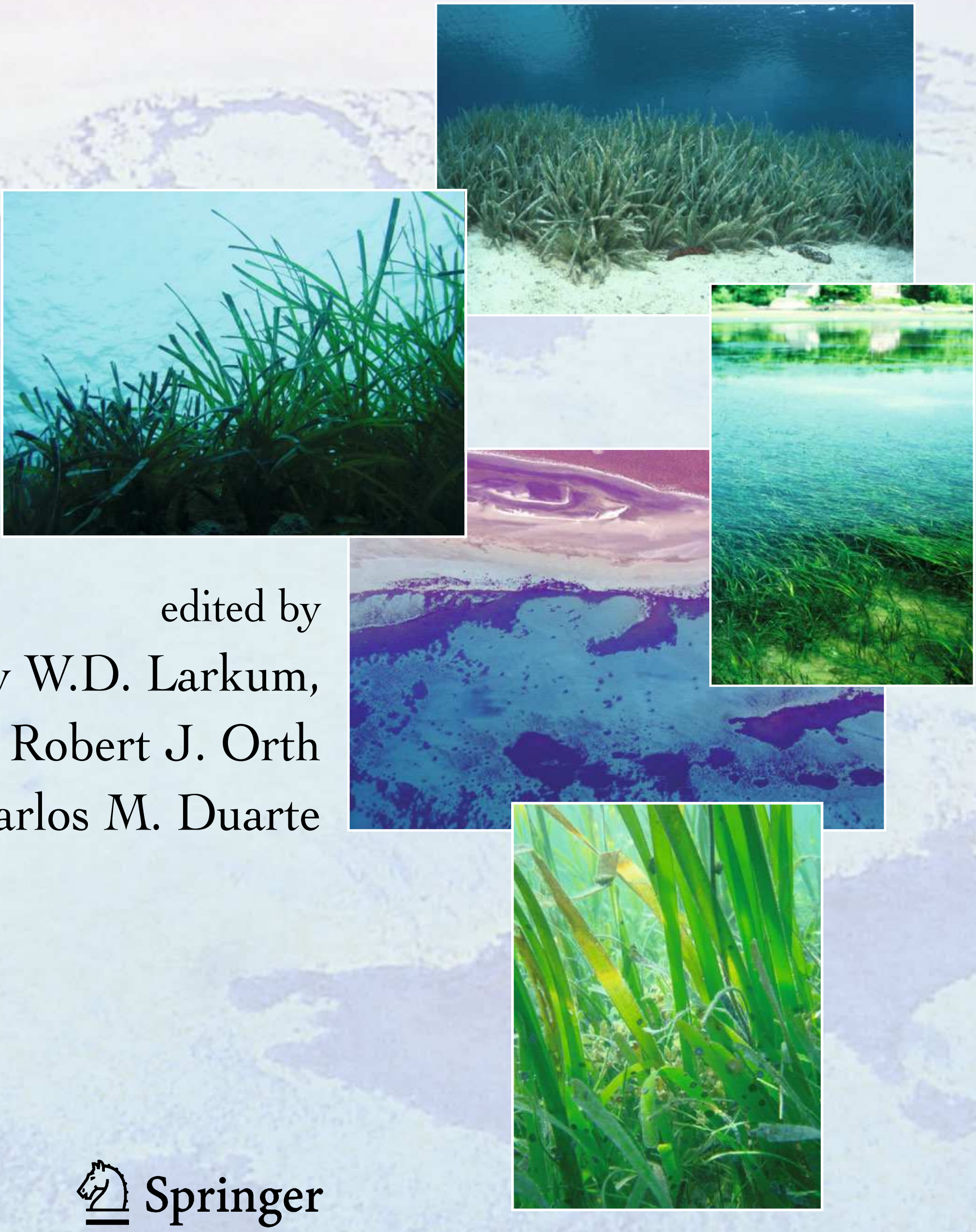
Seagrasses: Biology, Ecology and Conservation



edited by
Anthony W.D. Larkum,
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and Carlos M. Duarte

Springer

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by

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Contents

Foreword

Seagrasses have captured the imagination of scientists only relatively recently. Marine algae or seaweeds have had a much more glorious history, extending back to the 18th Century. It is true that Aristotle described the seeds of *Posidonia oceanica* and that, much later, Carl von Linné (Linnaeus) recognized and named two species of seagrass in 1779: *Zostera marina* (1753) and *Posidonia* (*Zostera*) *oceanica* (1757). However this knowledge penetrated very little, despite the fact that the savant and grandfather of Charles Darwin, Erasmus Darwin wrote a stanza on *Zostera* in his Botanic Garden (Part V) in 1803 (see also Fig. 5, Chapter 25):

> "Stretch'd on her mossy couch, in trackless deeps,
> Queen of the coral groves, *Zostera* sleeps;
> The silvery sea-weed matted round her bed,
> And distant surges murmuring o'er her head."

There were certainly pioneers of seagrass biology early in the second half of the 19th Century (notably, P. Ascherson) and early 20th Century (e.g. C.H. Ostenfeld and W.A. Setchell). And while the pandemic decline of eelgrass in the 1930's was widely noted along with loss of numerous ecosystem functions, seagrass science remained submersed for the next 40 years. It was not until the landmark publication of "Seagrasses of the World" by C. (Kees) den Hartog in 1970 that the taxonomy of seagrasses was in any way brought into line with systematic studies of most other plants over a century earlier. This was a seminal time as the advent of SCUBA diving led to a quantum leap forward in studies of the benthic components of the nearshore marine environment. A major result of this happy union of events was a sudden realization that seagrasses played a major role in nearshore ecosystems in all continents except Antarctica. This realization led to major funding initiatives such as the International Decade of Ocean Exploration, the launch of a journal in which seagrass biology played a major role (Aquatic Botany, 1975) and the launching of a series of Seagrass Workshops (the first in Leiden, 1973), which have focused the efforts of a growing cohort of seagrass researchers around the world (Seagrass 2004 and International Seagrass Biology Workshop 6, in Townsville, Australia, had 170 delegates). In addition the recent publication of an introductory book on Seagrass Ecology (Hemminga and Duarte 2000), a Global Seagrass Methods book (Coles and Short, 2003) and a Global Seagrass Atlas (Green and Short, 2003) have given researchers and managers alike a new set of tools to facilitate the further understanding of seagrasses. However, despite this upsurge in seagrass science, much remains unknown in seagrass biology and ecology. Seagrass research has been concentrated in only a few areas of the world (Australia, Europe, United States) and with only a few of the 50+ species (e.g. *Zostera marina*, *Posidonia oceanica*, *Thalassia testudinum*), with many existing paradigms developed from even fewer species and areas (Duarte 1999).

The need for increased understanding today has taken on a new meaning, and urgency, as the rate of seagrass loss appears to be accelerating concurrently with the rapid urbanization of the coastal zone, where seagrasses are most abundant (Green and Short, 2003). The very survival of seagrasses, which have been present for over 100 million years, now depends on a renewed commitment by all parties – managers, scientists, politicians, and the general public – to form partnerships to conserve remaining seagrass beds and restore, where possible, lost seagrass habitat. This renewal can only be successfully accomplished with a clear understanding of how all seagrasses grow and survive and how various fauna utilize this habitat. Thus, we as editors, believe the contents of this book are timely in this regard as they set the stage for what we must do to insure seagrasses not just survive but thrive in the face of rapid urbanization of the coastal zone. We believe by examining where we were with seagrass science, what is occurring presently, and where we must go is critical to this survival. In this book, we have not just asked our authors to review their area of specialty, but more importantly they were asked to reassess and reformulate paradigms and set the stage for how the field **must** develop if seagrasses are to persist.

So what, taxonomically, are seagrasses? This question is tackled in Chapters 1 and 2. However, as will be seen in those pages the answer is not so easy as we would like. Seagrasses are certainly the only flowering plants that are found in the sea and they belong to the Monocotyledons. They belong to at least two families, the Potomagetonaceae and the Hydrocharitaceae, and maybe more. However, in contrast to freshwater and land plants, there are relatively few genera (ca. 12) and these are very diverse, indicating that seagrasses have had a multi-pronged origin. Furthermore, when it is realized that many of these genera have species, which grow in estuaries and coastal lagoons alongside other hydrophytes, the real difficulty in defining seagrasses becomes apparent. Should one include the Ruppiaceae in the list of seagrasses and, if one does, why exclude certain members of the Zanichelliaceae? These arguments are set out in Chapter 1 and 2; yet surprisingly questions remain. Suffice it to say that up to the present time a pragmatic assessment has been made by the seagrass community that seagrasses are those flowering plants that occur in estuaries or on continental sea margins – and *Ruppia* and *Zanichella* species are only allowed in under sufferance, as these can complete their life cycles outside marine waters.

And this discussion begs the question as to the definition of a seagrass? This again is a contentious question. Apart from the systematic questions posed in Chapters 1 and 2, there is the question of what morphological characteristics do seagrasses possess in common. As discussed in Chapter 3, it can be seen that most of the individual characteristics of seagrasses are possessed by other hydrophytes. Not even the ability to live in increased salinity is a unique feature of seagrasses. Certainly they all possess the ability to pollinate underwater and most reproduce underwater. Most are adapted to the wave-prone environment of the sea, with tough linear leaves and an underground rhizome system, but the widely distributed genus *Halophila* is an exception here. The characteristics most often cited as unique to seagrasses are as follows:

- Live in an estuarine or marine environment, and nowhere else.
- Pollinate underwater with specialized pollen.
- Produce seeds underwater which can be dispersed by both biotic and abiotic agents .
- Have specialized leaves with a very reduced cuticle and an epidermis which lacks stomata and is the main photosynthetic tissue.
- Have a rhizome or underground stem which is important in anchoring.
- Have roots that can live in an anoxic environment and are dependent on oxygen transport from the leaves and rhizome but are also important in the nutrient transfer processes.

The importance of seagrasses as it emerged over the last quarter of the 20^{th} Century is in their key role on the shallow seaward margins of our continents. Seagrasses are now considered one of the important ‘ecosystem engineers’ (see Chapter 6) given their ability to change significantly numerous aspects of their environment. Their importance here is summarized in a set of axioms, which have become familiar to planners and conservationists, now often referred to as ‘ecosystem services’ (Costanza et al., 1997):

- Seagrasses are important primary producers, that is they convert sunlight and carbon dioxide efficiently into organic form;
- Seagrasses supply organic food to a variety of dependent food webs;
- Seagrasses stabilize the seabed in which they grow;
- Seagrasses structure the seabed on which they grow into a complex environment which provides places for many organisms to exist;
- Seagrasses act as the nursery ground for many commercially-caught species.

Are these axioms correct or are they “feel good” sayings that have been used to encourage the workers in the field. One of the recommendations to authors of chapters of this book was to challenge the current paradigms, and therefore the reader will find this reflected in many chapters. For example, the axiom that “seagrass ecosystems are driven by detritus” is challenged in Chapter 7 (Mateo et al.) where it is shown that production from epiphytic algae and benthic algae may well exceed that from the detrital production system of seagrasses.

Another area where science has made great progress is seagrass genetic structure. This is reflected in work on seagrasses and Chapter 2 (Waycott et al.) surveys the current status of seagrasses from this stand point. The result is a fresh approach to the taxonomy and systematizing of seagrasses. The reader will find that several important changes are recommended here; and in some cases a species or even a genus (*Heterozostera*) has disappeared (and at higher levels important changes are recommended). These changes have not at this time been accepted by many taxonomists. This is reflected in the stance of Chapter 1 (den Hartog and Kuo). It will be many years before many of these differences are resolved. As both approaches have their shortcomings, there has been no attempt in this book to be prescriptive: where differences do occur the reader is advised of the different approaches and is left to make up her/his mind on the subject.

Seagrasses are, *par excellence*, the plants that evolved hydrophilous pollination but only recently has a mechanistic approach been undertaken. Ackerman (Chapter 4) reviews the nature of pollination mechanisms and the unique adaptations these plants have evolved to insure successful pollination. And with successful pollination emerges the production of a seed, the unifying theme in all angiosperm species. Yet little is known about seeds, seed ecology and seed dispersal processes in seagrasses. Orth et al., (Chapter 5) review the scant but growing body of literature for seagrasses but more importantly, attempt to integrate emerging issues in the terrestrial realm and their applicability to seagrasses.

Seagrasses influence numerous processes and these are highlighted in a number of excellent chapters. Marba et al. (Chapter 6) review the role of seagrass beds on coastal biogeochemistry, by first examining their effect on particulate and dissolved materials (i.e. organic matter, dissolved inorganic carbon, carbonates, gases) in the water column and sediments of coastal areas, and (2) by examining the processes involved in mineralization of organic matter and nutrient cycling in sediments colonised by seagrasses. Mateo et al. (Chapter 7) describe carbon fluxes in seagrass ecosystems. Koch et al. (Chapter 8) examine hydrodynamics at scales ranging from molecules to ecosystems. Romero et al. (Chapter 9) highlight nutrient dynamics. Borum et al. (Chapter 10) review current status of knowledge with respect to oxygen production, consumption and transport within seagrasses, and briefly discuss the potential coupling between seagrass oxygen dynamics and the occurrence of die-off events in seagrass beds. And finally, Duarte et al. (Chapter 11) address processes and mechanisms responsible for the dynamics of seagrass meadows.

Light and photosynthesis and their measurement are dominant themes from the earliest papers in seagrass ecology. Yet this field has been rapidly evolving with the development of new tools leading to new discoveries about light and its measurement and the basis of light capture and the photosynthetic mechanisms. A series of chapters allow for the reader to follow in progression the science of light penetration into marine waters (Zimmerman and Dekker, Chapter 12), the influence of seagrasses on light absorption and light refection in shallow communities (Zimmerman, Chapter 13), the emerging role of remote sensing in seagrasses (Dekker et al., Chapter 15), and finally the importance of photosynthesis and the photosynthetic mechanisms of seagrasses (Larkum et al., Chapter 14).

Faunal and floral studies were also an important component in the early work by Japanese, American and European scientists and coincided with the many attempts to define community. This was followed by experimental work on the important interactions between plants and the many animals reported from seagrass beds. Borowitza et al. (Chapter 19) review the literature on epiphyte diversity and abundance. Valentine and Duffy (Chapter 20) provide an important synthesis of the grazing world, both macro and meso-grazers, and their important direct and indirect interactions at varying spatial scales. Gillanders (Chapter 21) explores the latest developments in fisheries utilization, including new techniques for assessing habitat linkages (e.g. otolith chemistry) and how important seagrass beds are to fish production. Finally Heck and Orth (Chapter 22) succinctly summarize the previous generalizations that continue to be supported by recent work, and then focus attention on results that challenge the conventional wisdom on predator-prey interactions in seagrass meadows.

Research in the 1970's in Europe, United States and Australia showed the devastating negative influence of anthropogenic factors on seagrass distribution and abundance. Loss of seagrasses has continued at an alarming pace as human habitation of the coastal zone rapidly expands. Walker et al. (Chapter 23) detail aspects of more recent research demonstrating changes, both negative and positive, in seagrass distributions, as revealed by mapping and other detailed investigations. Ralph et al. (Chapter 24) provide an overview of the current understanding of how anthropogenic contaminants impact seagrasses, the ecophysiological responses of seagrasses and finally describe how modeling can be used to manage contaminant loads (specifically nutrients) in the process of seagrass recovery. Kenworthy et al. (Chapter 25) examine the current state of seagrass science within the viewpoint of conservation biology, discussing areas where seagrass science is developing a conservation biology approach, identifying priority research topics for conservation science in the future, citing examples where science and conservation biology are being applied in the seagrass biome, and finally recommending a course of action based on the principles of conservation biology to reverse the global trend of fragmentation, local extinction, and general degradation of the seagrass biome. Finally, Bell et al. (Chapter 26) bring into focus a new approach to studying seagrasses in relation to the entire landscape, by first providing a brief review of concepts and techniques associated with a landscape approach, then evaluating how information collected from studies in seagrass systems compares to that from analogous terrestrial systems/landscapes. Finally, they discuss some potential areas of future research in the field of seagrass landscape ecology, recommending conceptual and methodological improvements.

Last, a significant amount of research has been conducted on three genera, *Thalassia*, *Posidonia* and *Zostera*, which together account for much of the world's seagrass meadows Three knowledgeable groups of scientists have attempted to synthesize the important aspects of significant research on these three genera with the hope that research in the other nine genera will follow suit.

The science of seagrasses has made tremendous strides in the last two decades but much remains ahead. We hope the chapters in this book both provide the necessary background on what brought each topic to where it is today and indicate where future research needs to go to advance the field to the next level. If we have accomplished that, then we, as editors, will feel we have done our job in this book.

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Chapter 1

Taxonomy and Biogeography of Seagrasses

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I. Introduction

Seagrasses are aquatic angiosperms, which are confined to the marine environment. The term seagrass (with several linguistic variants in the Germanic language group) refers undoubtedly to the grass-like habit of most of its representatives. The term has been long used by fisherman, hunters, farmers, and other inhabitants of the coastal areas of several European countries, i.e. areas where only species occur with long linear leaves. Ascherson (1871) probably was the first researcher to introduce the term into the scientific literature.

The seagrasses form an ecological group, and not a taxonomic group. This implies that the various seagrass families do not necessarily have to be closely related.

The taxa regarded as seagrasses belong to a very limited number of plant families, all classified within the superorder Alismatiflorae (Monocotyledonae) (Dahlgren et al., 1985), also generally known as the Helobiae (Tomlinson, 1982). The subclass Alismatanae (Kubitzki, 1998) is with respect to its contents identical with Alismatiflorae. Three out of four families consist exclusively of seagrasses, viz. the **Zosteraceae**, the **Cymodoceaceae**, and the **Posidoniaceae**. In the past these families generally have been classified as subfamilies of the **Potamogetonaceae** (Ascherson and Graebner, 1907; den Hartog, 1970). Further studies have shown that the latter family appeared to be too heterogeneous (Tomlinson, 1982; Dahlgren et al., 1985), and had to be split. So, apart from the Potamogetonaceae *sensu stricto*, all of the former subfamilies were upgraded to the family level. In fact some authors had already long ago recognized the special identity of these families, e.g. Dumortier who described the Zosteraceae as early as 1829 as an independent family beside the Potamogetonaceae *sensu stricto*, and the Zannichelliaceae. A fourth family, the **Hydrocharitaceae**, contains three genera that are considered seagrasses, but the other 14 genera in this family are confined to fresh-water habitats (Cook, 1990, 1998).

Apart from the families mentioned above which have altogether 12 marine genera there are no other genera that are fully confined to the marine environment. In other aquatic plant families so far only two species have been found that occur exclusively in marine habitats, viz. *Ruppia* aff. *tuberosa* of the family **Ruppiaceae**, and *Lepilaena marina* of the family **Zannichelliaceae** (Kuo and den Hartog, 2000). The inclusion of these two species within the seagrasses is still a matter of debate. Descriptions of these families and genera have been included in the treatment of the monocotyledonous flowering plants edited by Kubitzki (1998) (Hydrocharitaceae by Cook; Ruppiaceae and Najadaceae by Haynes, Holmberg-Nielsen and Les; Potamogetonaceae and Zannichelliaceae by Haynes, Les and Holm-Nielsen; Cymodoceaceae, Posidoniaceae and Zosteraceae by Kuo and McComb). Furthermore, brief descriptions of all presently described seagrass species, as well as a key for the identification of them, have been provided by Kuo and den Hartog (2001).

Arber (1920) formulated a set of four properties, which in her opinion were considered to be

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indispensable for a marine water plant. These properties can be listed as follows: (i) the plants must be adapted to life in a saline medium; (ii) the plants must be able to grow when fully submerged; (iii) the plants must have a secure anchoring system; and (iv) the plants must have a hydrophilous pollination mechanism. It is obvious that seagrasses fulfil these requirements; they are able to achieve their vegetative as well as their generative cycle, when fully submerged in a saline medium. This set of properties is, however, not complete, as there are several other taxa of aquatic plants that also satisfy the four criteria listed by Arber, although they do not normally occur in marine habitats; nevertheless, they do even better in fact than the seagrasses where salinity tolerance is concerned (den Hartog, 1970). They form the 'eurysaline' group (den Hartog, 1981), an ecological group of aquatic plants, that is characteristic for waters with an unstable salinity, such as mixo- and hyperhaline brackish waters, continental salt waters where the dominant anion can be chloride, sulfate or even hydrocarbonate (therefore the term 'saline' is used, to distinguish it from 'haline' which refers to chloride dominated waters with a marine character); some of these taxa can occur in hard fresh water, and there are observations of some of them from extremely oligotrophic fresh waters. It is also known that representatives of this group can withstand very large and very sudden fluctuations in environmental parameters, such as salinity and temperature, and in contrast to the true seagrasses their seeds are resistant to protracted desiccation. Although the representatives of this group may be found in coastal areas their general distribution is not maritime; their altitudinal range is from sea level up to 4000 m in mountains. The eurysaline group consists of taxa from three monocotyledonous families, the **Ruppiaceae** (with the genus *Ruppia*), the **Zannichelliaceae** (with the genera *Zannichellia*, *Lepilaena*, *Althenia*, and *Pseudalthenia*), formerly classified as subfamilies of the Potamogetonaceae, and the **Potamogetonaceae** *sensu stricto* of which only *Potamogeton* subgen. *Coleogeton* (by some authors considered to be an independent genus, *Stuckenia*) is involved. Several other aquatic plant families have developed species with a rather wide salt tolerance, e.g. *Najas marina* in the Najadaceae (which recently has been shown to be part of the Hydrocharitaceae), and *Ranunculus baudotii* in the Ranunculaceae, a dicotyledonous family. So the true seagrasses are characteristic for homoiohaline marine habitats, while the members of the eurysaline group occur in poikilosaline waters. It appears, that these eurysaline species can live under marine circumstances, but are usually not able to compete successfully with the seagrasses. According to den Hartog (1970) it is probably a basic rule in ecology that a wide tolerance for environmental fluctuations is coupled with a reduced capacity to compete with more stenobiontic taxa under more or less stable circumstances. The capacity to compete successfully with other organisms in the marine environment is thus another basic property of seagrasses.

It has to be pointed out that not all seagrasses are stenohaline to the same degree. Particularly some members of the genera *Zostera*, *Cymodocea*, *Halodule*, and *Halophila* may penetrate to some extent into estuaries, and these are the same ones that extend up to the middle of the intertidal zone. This means in practice that under estuarine conditions and in the intertidal belt true seagrasses and eurysaline water plants may meet, just as further upstream eurysaline species may come into contact with fresh-water plants. In the Baltic (Samuelsson, 1934; Luther, 1951a,b) and in the Black Sea (Milchakova, 1999), which both show a reduced salinity and a considerable salinity gradient, mixed stands of seagrasses and eurysaline aquatics have been commonly recorded.

It is our intention to present here the taxonomy of the seagrasses at the family and the genus level, including also descriptions of the families of the poikilosaline group which have a true marine representative. The author's names of the species, accepted as valid, are given in the 'List of the seagrass species of the world' (see Appendix A p. 22–23).

II. Key to the Angiosperm Families Containing True Marine Species

1a. Leaves differentiated into a sheath and a blade, without a ligule, or a blade with a clear petiole. 2
1b. Leaves differentiated into a sheath and a blade, with a ligule. 3
2a. Flowers dioecious, (sometimes monoecious) with a trimerous perianth. Pollen spherical, free or arranged within a moniliform string. . . . . Marine **Hydrocharitaceae**
2b. Flowers monoecious, in pairs on a peduncle, each with two anthers and 4-many ovaries, but

without a perianth. Pollen boomerang-shaped, free. . . . . **Ruppiaceae**

3a. Inflorescence cymose, with the branches ending in 'spikes'. Flowers actinomorphous, bisexual, consisting of three stamens with large connectives and one ovary with a sessile, disc-shaped stigma. Tannin cells present . . . **Posidoniaceae**

3b. Flowers simple, unisexual, consisting of 1 or 2 ovaries or a single stamen, arranged within a specialized inflorescence or just single or in pairs. Stamens with reduced connectives. Ovary bearing a style with 1, 2, or 3 stigmata. Tannin cells present or absent. 4

4a. Flowers, unisexual or bisexual, arranged in two rows on one side of a flattened spadix enclosed in a spathe. Stamens consisting of two extrorsely dehiscent thecae, connected by a ridge-like connective. Ovary horizontally placed, with a short thick style and two stigmata shed after flowering. Tannin cells absent. . . . . **Zosteraceae**

4b. Flowers unisexual, solitary, in pairs or as a cluster on a common pedicel, terminating a short branch. Tannin cells present or absent. 5

5a. Leaves with 3-many nerves and numerous tannin cells. Flowers unisexual, without a perianth, solitary or in pairs, or arranged within a cymose inflorescence. Male flowers sessile or stalked consisting of two, dorsally connate anthers. Pollen filiform. Ovaries in pairs with 1, 2, or 3 filiform styles. Tannin cells present. . . . . **Cymodoceaceae**

5b. Leaves very narrow, with only one central nerve, without tannin cells. Flowers terminal. Male flower consisting of a stalked anther, often with a small scaly perianth. Female flower consisting of 1–8 free carpels on a joint pedicel, surrounded by a scaly perianth. Styles peltate or feathery. Pollen spherical. Tannin cells absent . . . . **Zannichelliaceae**

III. Seagrasses: General Taxonomy

Zosteraceae

Zosteraceae Dumortier, Anal. Fam. Pl. (1829) 65, 66; nom. cons.
Typus: *Zostera* L.

Monoecious or dioecious marine plants. Rhizome creeping, herbaceous, monopodial or sympodial; when monopodial with two vascular bundles in the cortical layer and at each node two or more unbranched roots and a leaf or a prophyllum, with in its axil a short lateral branch bearing a bunch of distichously arranged leaves; roots and rhizomatic leaves alternating; when sympodial (*Heterozostera*) with 4–10 vascular bundles in the cortical layer and at each node two unbranched roots and an erect stem with distichously arranged leaves and without roots at its nodes. Leaves linear, differentiated into a sheath and a blade with a ligule. Leaf sheath compressed, amplexicaulous, ligulate, either membranous and tubular or open and then auriculate with scarious flaps. Leaf blade linear, with 3–9(-11) parallel nerves and with several accessory bundles between every two of these; nerves connected by perpendicular cross-veins, margin entire, sometimes slightly denticulate or provided with a fringe of uncolored, sclerenchymatic 'fin cells'; tip variable in shape. Generative shoot terminal or lateral, sympodial, erect, consisting of a panicle of rhipidia, but often reduced to a single rhipidium; each rhipidium consisting of 2–5 spathes, but sometimes reduced to a single one; peduncle of each spathe partially coalescent with the axis from which it springs or completely free. Spathe consisting of a sheath and a blade; spathal sheath ligulate, open with two more or less overlapping, auriculate flaps, enclosing a sessile or stalked spadix on the dorsal side of which in *Zostera* and *Heterozostera* the male flowers (stamens) and female flowers (gynoecia) are alternately arranged. Stamens consisting of two free, bilocular, extrorsely length-wise dehiscent, deciduous thecae connected by a reduced ridge-like connective, without a filament; pollen confervoid. Retinacula intramarginal, one beside each stamen, sometimes absent (*Zostera* subgen. *Zostera*); on the female spadices of *Phyllospadix* alternating with the gynoecia. Gynoecium consisting of a superior, horizontally placed, ellipsoid or crescent-shaped ovary with a short thick style and two stigmata of which the distal parts are shed after fertilization; ovule 1, orthotropous, pendulous. Fruit indehiscent, ovoid or ellipsoid with scarious pericarp or else crescent-shaped with the pericarp differentiated into a soft exocarp and a hard fibrous endocarp. Seed 1, ovoid or ellipsoid; embryo macropodous consisting for the larger part of the hypocotyl, which is ventrally grooved; in this groove the short, straight, tubular cotyledon which serves as a sheath for the plumula; primary root usually not developing; endosperm absent. Tannin cells absent.

The family consists of three genera, viz. *Zostera*, *Heterozostera*, and *Phyllospadix.*

There is no doubt about the monophyletic status of the family Zosteraceae. This has already been concluded by Tomlinson (1982) on merely anatomical and morphological grounds. A further confirmation comes from molecular phylogenetic studies of the families of the subclass Alismatidae, using chloroplast *rbc*L (Les et al., 1997; Procaccini et al., 1999a). Les et al. (1997) demonstrated that the Zosteraceae are more closely related to the Potamogetonaceae and the Zannichelliaceae than with the other seagrass groups. These studies, however, did not support the recognition of *Heterozostera tasmanica* as representing a distinct genus, but accepted it as a distinct species within the subgenus *Zosterella* (Les et al., 1997, 2002). Based on the *matK* gene sequence data, Tanaka et al. (2003) also show a similar result. On the other hand, Kato et al. (2003) proposed to divide the Zosteraceae into three genera: *Phyllospadix*, *Zostera* and *Nanozostera*, the genus *Nanozostera* containing two subgenera, *Zosterella* and *Heterozostera*. In this case, by priority *Heterozostera,* which was established more than 30 years earlier, should be used as the generic name instead of *Nanozostera*. There is nothing known about the possible ancestors of the family. Originally it was thought that *Archeozostera* (Koriba and Miki, 1931, 1960) from the Cretaceous of Japan was a protozosterid (den Hartog, 1970), but Kuo et al. (1989) have shown convincingly that *Archeozostera* is not a seagrass at all, and possibly not even a plant.

Key to the Genera

1a. Rhizome monopodial, herbaceous, with two vascular bundles in the cortical layer; a short lateral branch at each node. 2

1b. Rhizome sympodial, but sometimes monopodial, often ligneous, with 4–10 vascular bundles in the cortical layer. Stems erect, not branched, with distichous leaves . . . . ***Heterozostera***

2a. Monoecious. Spadix always enclosed within the spathal sheath. Retinacula, if present, membranous, not nerved, smaller than the ovaries or stamens. Peduncle of the spathe partly coalescent with the axis from which it springs. Fruit ovoid or ellipsoid. Rhizome with elongate internodes, and with two, or more, long, thin roots at each node. Vegetative parts not sclerenchymatic. Leaf-blades thin, translucent; margin entire or rarely slightly denticulate. Sheaths deciduous; sometimes some scaly basal parts remaining. . . . . ***Zostera***

2b. Dioecious (rarely monoecious). Spadix, when mature, projecting out of the spathal sheath. Retinacula coriaceous, one-nerved, larger than the ovaries or stamens. Peduncle free. Fruit crescent-shaped. Rhizome with very short, thick internodes, and with two or more thick roots at each node. Vegetative parts usually strongly sclerenchymatic. Leaf-blades coriaceous, with ‘fin cells’ along the margin. Basal parts of the sheaths decaying with age into bundles of very fine, woolly fibres . . . . ***Phyllospadix***

Zostera L. Sp. Pl. ed. 1 (1753) 986.
Type species: *Zostera marina* L.

The genus consists of two well-distinguished subgenera, *Zostera* and *Zosterella*.

In subgen. *Zostera* the rhizome has the fibre bundles in the outermost part of the cortex, and there are always two groups of roots at each node; the leaf-sheaths are tubular and rupturing with age; the generative shoots are terminal and retinacula are absent. In the old literature this subgenus is referred to as subgen. *Alega*; according to the rules of botanical nomenclature the correct name is subgen. *Zostera*, as it contains the type of the genus. In subgen. *Zosterella* (Ascherson) Ostenfeld (type species *Z. nana* Mertens ex Roth = *Zostera noltii* Hornemann) the fibre bundles occur in the innermost layers of the outer cortex of the rhizome; the leaf-sheaths are open with two membranous flaps; the generative shoots develop lateral and in the inflorescences the retinacula are always present. Recently, Tomlinson and Posluszny (2001) upgraded the latter subgenus to a genus in its own right, *Nanozostera*, mainly because they considered the differences between this taxon and the subgenus *Zostera* of the same order as its differences with *Heterozostera*. Meanwhile Kuo (2005) has discovered that the genus *Heterozostera* is also not homogeneous from a morphological point of view.

The subgenus *Zostera* is widely distributed in the northern temperate coastal waters of the Atlantic and the Pacific. Up to now four species have been accepted (den Hartog, 1970), but a further analysis may show that this number is too low. At present

Z. marina has been recorded from both sides of the northern Atlantic and both sides of the northern Pacific. The species *Z. caespitosa* and *Z. caulescens* are restricted to the Asiatic side of the Pacific; *Z. asiatica* described from the north-eastern Pacific may be identical with the wide-leaved form of *Z. marina*, earlier described as *Z. latifolia* and *Z. oregona*. The record of *Z. asiatica* by Phillips and Willey-Echeverria (1990) for the Pacific coast of North America may refer to *Z. latifolia* or *Z. oregona*. Regrettably the few distinguishing characters intergrade, and hamper the definition of clear-cut taxa. Backman (1991) recognized five varieties of *Z. marina* along the Pacific coast of North America, and formally described these. However, he also did not discuss the relationship of these varieties, if any, with the taxa related to *Z. marina*, earlier described from the same area, such as *Z. oregona, Z. latifolia* or *Z. pacifica*, nor is there any indication that his *Z. marina* var. *typica* has any relation to the original specimens of this species that was described from Europe. In Europe *Z. marina* is also not a sharply defined species. There occur perennial, biennial, and annual populations. The annual form has been recorded by some authors as a separate species, *Z. angustifolia*; others consider it at the variety level or as an example of the variability of the species, because of the lack of reliable distinguishing morphological characters. Van Lent and Verschuure (1994) found that there is a continuum between the annual and perennial populations; some appear to be truly annual, in others part of the plants appears to be biennial, i.e. at least surviving the winter season; and a third group of populations is permanently green. These differences in life cycle were found in a small area in the same estuary in The Netherlands. It has also to be mentioned, that various populations along the European coast show considerable differences in their temperature and salinity tolerance. Further taxonomic research in this subgenus is necessary.

The subgenus *Zosterella* is widely distributed in the warm temperate coastal waters of the seas of the northern and the southern hemisphere, with some incursions in tropical waters and one species extends into the cold temperate zone. In the Atlantic, including the Mediterranean only one species, *Z. noltii* occurs. It has been recorded also from the land-locked Caspian Sea and the Aral Sea. In the northern Pacific the subgenus is represented also by only one species, *Z. japonica*, which extends from the Siberian east coast down to Vietnam. Quite recently this species has colonized the Pacific coasts of Canada and the USA. In the southern hemisphere *Z. capensis* occurs from the Cape Province up to Kenya. In temperate Australia three species occur, *Z. muelleri, Z. mucronata,* and *Z. capricorni*, which more or less exclude each other geographically. *Z. muelleri* inhabits the coasts of Victoria, Tasmania and the eastern part of South Australia, *Z. mucronata* is restricted to the eastern coasts of South Australia and the southern and south-western part of Western Australia, and *Z. capricorni* is distributed along the eastern coast of Australia up to Papua New Guinea. Moreover, it occurs in New Zealand, together with *Z. novazelandica*.

Les et al. (2002) carried out a phylogenetic study on the Australian and New Zealand Zosteraceae using DNA sequences from nuclear (ITS) and plastid (*tmk* intron, *rbc*L) genomes (see also Waycott et al., Chapter 2). These molecular studies did not support the distinctness of *Zostera capricorni, Z. mucronata, Z. muelleri*, and *Z. novazelandica* as four discrete species, but indicated that some isolation by distance had occurred. The *mat*K gene sequence data of Tanaka et al. (2003) also show that *Z. muelleri, Z. capricorni, Z. novazelandica*, and *Z. mucronata* belong to the same lineage. However, Tanaka et al. (2003) also unexpectedly found *Z. capensis* is not associated with the other above mentioned *Zostera* species but belongs to the same lineage as *H. tasmanica*. In the meantime, Les et al. (2002) further conducted a cladistic analysis of 31 morphological, vegetative and reproductive characters, based on data from 15 previous publications of seven species of *Zostera* subgen. *Zosterella*, to conclude that there are no morphological differences between these species. Based on molecular and cladistic evidence Les et al. (2002) recommended that all Australian *Zostera* species should be merged taxonomically as a single species, which in that case by priority should be called *Z. muelleri*, and not *Z. capricorni*, as proposed by Les et al. (2002), as this latter species has been described nine years later. Regretfully, this error has already been applied in the most recent literature (Green and Short, 2003). On the other hand, Kato et al. (2003) retained all described *Zostera* and *Heterozostera* species but wrongly placed these species under the genus *Nanozostera*. As discussed above a taxonomic mistake has been made by choosing *Nanozostera* instead of *Heterozostera*.

In our opinion the three Australian species are in general well distinguished by morphological differences in their leaf-tip and nervation. The shape of the leaf apex, in spite of having considerable variation, still is one of most important vegetative characters for identification of these *Zostera* species. Further *Z. capricorni* has leaves with five longitudinal nerves, while the other two species have only three. An other important fact is, that the three species have each a different area of distribution with only marginal overlap. In these areas of overlap intermediate forms occur, but these may be the result of hybridization. We certainly do not deny that the species are closely related. Robertson (1984) noticed also that a broad spectrum of intergrades occurs and recommended further basic taxonomic work to elucidate the *Z. mucronata–Z. muelleri–Z. capricorni* complex. Turner et al. (1996) also could not decide the species status of their studied *Zostera* material from New Zealand.

However, Les et al. (2002) echoed Robertson's (1984) suggestions recommending 'common garden experiments to be conducted among these species' to see whether those leaf tip and other morphological characters are the result of environmental conditions, or are genetically determined, or both. Until such fundamental data are available, we recommend here that at least *Z. muelleri, Z. capricorni*, and *Z. mucronata* should continue to be recognized. McMillan (1982) investigated five *Zostera* species, amongst which four members of the subgenus *Zosterella*, and found that each species presented a different isozyme pattern.

Further, it should be noted that three out of 31 characters separate *Z. noltii* and *Z. japonica* (see Les et al., 2002), but the *mat*K tree shows a close affinity of these two species, which have disjunct distributions (Tanaka et al., 2003).

Robertson (1984) recognized two ecotypes of *Zostera muelleri* from south-eastern Australia, one in the intertidal belt of sheltered bays, and a more robust estuarine form in lagoons and more or less land-locked waters, which is almost permanently submerged. She stressed that numerous intergrades occur between them. Similar observations have been made for other *Zostera* species, e.g. *Z. noltii* in western Europe, Mauritania, and the Mediterranean, *Z. capricorni* in New South Wales, and *Z. capensis* in South Africa.

Phyllospadix Hooker, Fl. Bor. Am. 2 (1838) 171

Type species: *Phyllospadix scouleri* Hooker

The genus contains five species, all occurring along the northern temperate coasts of the Pacific. The genus is rather homogeneous, although two groups of species can be recognized. One group consists of the two species, *P. scouleri* and *P. torreyi*, and occurs along the west coasts of Canada, the USA, and Baia California. It is characterized by having rhizome nodes with 6–10 roots (in two rows), leaves with only three nerves (*P. japonicus* belonging to the other group also has three nerves), and generative axes consisting of one to several internodes and bearing one or more pedunculate spathes. The second group has three species, distributed in cold temperate waters in eastern Asia (*P. iwatensis* and *P. japonicus*) and North America from the Aleutic Islands southward to Oregon (*P. serrulatus*). In these three species the rhizome nodes have only two roots, and the generative axes are reduced to short pedunculate spathes.

Tsvelev (1981) erected a special section, *Phyllospadix* sect. *Sagitticarpus*, to include *P. torreyi*, because its inflorescence produces numerous spathes, without considering the infrageneric classification of the other species of the genus. Although we can recognize within the genus two species groups there is in our opinion no reason to subdivide *Phyllospadix* into sections or subgenera. If these groups have to be formally upgraded to the section level, the group which contains the type species should be named in accordance with the rules of the botanical nomenclature *P*. sect. *Phyllospadix* and *P*. sect. *Sagitticarpus* is in that case a superfluous synonym.

Further, it should be mentioned here that Tsvelev (1981) described two new species, *P. juzepczukii* and *P. ruprechtii* from eastern Russia and California respectively. Unfortunately, we have not been able to see material from these species. It appears that the leaves of *P. juzepczukii* have only three nerves, as in *P. japonicus*, and these taxa may possibly be identical, but in that case the species would show a very remarkable disjunct area of distribution. As far is known to us *P. japonicus* is restricted to the Honshu coast of the Japanese Sea, but is absent from Hokkaido, Korea and China. *P. juzepczukii* seems to be widely distributed in the northern Far East. It is clear from the diagnosis of *P. ruprechtii* that this species is synonymous with *P. scouleri*. Finally, Dawson et al. (1960) have found some 3-nerved, almost perfectly cylindrical leaf fragments of a *Phyllospadix* specimen along the coast of Baia California, Mexico.

Heterozostera (Setchell) den Hartog, Sea-grasses of the world (1970) 114
Type species: *Zostera tasmanica* Martens ex Ascherson (= *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog)

The genus has been originally erected to classify the rather aberrant *Z. tasmanica.* All previous researchers (den Hartog, 1970; Tomlinson, 1982; Les et al., 1997; Tomlinson and Posluszny, 2001) treated *Heterozostera* as monotypic and having distinct vegetative wiry erect stems and more than two vascular strands in the rhizome cortex. More material has now become available for study and the concept of the monotypic genus has to be reconsidered. The most recent revision of *Heterozostera* demonstrates that it is represented by three distinct taxa in Australia, and a fourth in South America (Kuo, 2005). All three Australian species have numerous cortical vascular bundles in the rhizome cortex, but only one of them possesses 'wiry erect stems'. Within the genus two distinct species groups can be distinguished which possibly have to be ranked as sections or subgenera. It is interesting to mention that Les et al. (2002) observed a low level of molecular divergence (ITS and *tmK*) between the *Heterozostera* population from eastern (one collection) and western (four collections) Australia. Due to a lack of morphological evidence (which they did not consider) to support this molecular finding, they concluded that this molecular difference was due to a relatively prolonged geographical isolation of the two populations rather than as clear evidence of a speciation event.

Cymodoceaceae

Cymodoceaceae N. Taylor in N. Amer. Fl. 17 (1909) 31; nom. cons.
Typus: *Cymodocea* König

Dioecious marine plants. Rhizome creeping, either herbaceous, monopodial, and rooting at the nodes (*Cymodocea*, *Syringodium*, *Halodule*) or ligneous, sympodial, and rooting from the internodes (*Amphibolis*, *Thalassodendron*). Scales scarious, ovate or elliptic, marked with more or less small, dark, longitudinal stripes, and dots (tannin cells). Leaves distichous. Leaf sheath broad, completely or almost completely amplexicaulous, leaving open or closed circular scars when shed, bi-auriculate, ligulate; scarious flaps covered with numerous short dark, longitudinal stripes, and dots (tannin cells). Leaf blade linear or subulate with three to several parallel or pseudoparallel (*Amphibolis*) nerves; parallel with the nerves more or less, short, dark, longitudinal stripes, and dots (tannin cells); leaf-tip variable in outline. 'Flowers' without perigone, solitary, either terminal on a short branch or arranged in a cymose inflorescence (*Syringodium*). Male 'flowers' subsessile or stalked, consisting of two quadrilocular, extrorsely dehiscent anthers, which are dorsally connate over at least a part of their length and are attached either at the same height or at a slightly different level (*Halodule*). Pollen confervoid. Female 'flowers' sessile or shortly stalked, consisting of two free ovaries each with either a long style (*Halodule*) or a short style, which is divided into 2 or 3 loriform stigmata. Ovule 1, suborthotropous, pendulous. Fruit either with a stony pericarp, more or less compressed (*Cymodocea*, *Halodule*, *Syringodium*) or with a stony endocarp and a fleshy exocarp from which four cuneate spreading lobes grow out (*Amphibolis*) or consisting of a fleshy bract which encloses the fertilized ovaries (*Thalassodendron*); not dehiscent. Seed 1. Embryo either consisting for the larger part of the plumula with a lateral primary root and a cylindrical hypocotyl, appressed to the upper part of the plumula (*Cymodocea*) or consisting of a long hypocotyl and a short plumula without a primary root (*Amphibolis*).

The family contains five genera: *Halodule*, *Cymodocea*, *Syringodium*, *Thalassodendron*, and *Amphibolis.*

From a morphological point of view the family is homogeneous, and monophyletic. In the past it has often been combined with the Zannichelliaceae, e.g. by Hutchinson (1934). The five genera are all well distinguished and there is no controversy about their status as is the case in the Zosteraceae. The family is old, as there are several fossil records of members of the genus *Cymodocea* from Eocene and Miocene deposits. *Thalassocharis* from the Cretaceous of The Netherlands and Germany has been considered as being a seagrass by Voigt and Domke (1955) and den Hartog (1970) did not reject this conclusion, but remarked that the stiff compact stems and the absence of aerenchymatic tissue show that *Thalassocharis* was not yet very well adapted to life in the aquatic environment. Kuo and den Hartog

(2000) did not regard *Thalassocharis* as a seagrass anymore.

In spite of the great differences in the morphology and the anatomy of their reproductive structures as well as their modes of pollination, Les et al. (1997) treated the families Cymodoceaceae, Posidoniaceae and Ruppiaceae together as one phylogenetic unit, the 'Cymodoceaceae complex', to distinguish it from the other seagrass groups such as the Zosteraceae and the marine Hydrocharitaceae.

Within the family two groups of genera can be recognized. *Halodule, Cymodocea,* and *Syringodium* have a monopodial rhizome, are herbaceous, and have leaf-blades that are shed before the leaf-sheaths. *Thalassodendron* and *Amphibolis* have a sympodial, ligneous rhizome, and the leaf-blades are shed with the sheaths as single units; further, these two genera show vivipary. There is, however, in our opinion no reason to give these groups a formal taxonomic status.

Key to the Genera

1a. Rhizome monopodial, herbaceous, with a short erect stem at each node. Leaf-sheath persisting longer than the leaf-blade. Anthers stalked. . . 2

1b. Rhizome sympodial, ligneous, with elongate, more or less branched, erect stems at certain nodes. Leaf-blade shed with its sheath. Anthers subsessile. 4

2a. Leaves flat. Flowers solitary. 3

2b. Leaves subulate. 'Flowers' arranged into a cymose inflorescence. . . . . ***Syringodium***

3a. Nerves 3. Anthers not attached at the same height on the peduncle. Ovary with one undivided style . . . . ***Halodule***

3b. Nerves 7–17. Anthers attached at the same height on the peduncle. Style divided into two stigmata. . . . . ***Cymodocea***

4a. Rhizome with two unbranched or little branched stems at every fourth rhizome node; roots 1–5 on the node preceding the stem-bearing one. Leaves with parallel nerves and denticulate apex. 'Flowers' enclosed by four leafy bracts. Anthers connate over their entire length, each crowned with one appendage. Style with two stigmata. False fruit composed of 1 or 2 fertilized ovaries surrounded by the enlarged inner bract . . . . ***Thalassodendron***

4b. Rhizome with 1–2 branching roots at each node and at a distance of (1-) 4–8 nodes one profusely branched stem. Leaves entire, with pseudoparallel nerves, and a bidentate apex. 'Flowers' enclosed by normal leaves. Anthers connate with their lower parts, each crowned with 2–3 appendages. Style with three stigmata. 'Fruit' consisting of one fertilized ovary with four pectinate, spreading lobes arising just above its base; viviparous. . . . . ***Amphibolis***

Halodule Endl., Gen. Pl. suppl. 1 (1841) 1368.
Type species: *Diplanthera tridentata* Steinheil (= *H. uninervis* (Forssk.) Ascherson).

The typification of *Halodule* has been complicate. Du Petit Thouars (1806) was the first to describe the genus from Madagascar under the name *Diplanthera*, but he unfortunately did not add a species name to his material. Steinheil (1838) described the material as *D. tridentata*. Steudel (1840) referred to the same material and named it, without a description, *D. madagascariensis*. He recognized a second species, *D. indica* that turned out to be *Halophila ovalis*. From Steudel's work it becomes also obvious, that the genus name *Diplanthera* has been used also for other genera in very different families. Endlicher (1841) referred to the material of Du Petit Thouars (1806) and the work of Steinheil (1838) as he founded the genus *Halodule*, but regrettably he failed also to transfer the species name to the new genus. Miquel (1855) was the first to describe a species in the genus as *H. australis*, for material from Indonesia, similar to Steinheil's species; therefore, the new epithet was superfluous. It took till 1882, before this material was properly named.

The genus consists of seven species. The main characters used for the identification of the species are the shape of the leaf tip and the width of the leaves (den Hartog, 1970). There are too few data of the generative structures, and the degree of variation of these is not yet clear; at present they cannot be used to identify the taxa. Moreover, they are not known for several taxa.

H. uninervis commonly occurs in the tropical Indo-West Pacific with a narrow- and a wide-leaved form. It is possible that these two forms represent different taxa; in that case the name *H. uninervis* is linked to the wide-leaved form, while the narrow-leaved form should be named *H. tridentata* (Steinheil) F. von Mueller. In the West Pacific a second species, *H. pinifolia*, occurs as well; in the

Indian Ocean it is less common and restricted to India. In the Caribbean *H. wrightii* is widely distributed from Cuba and the smaller Antilles; along the coast of South America it crosses the mouth of the Amazon River, and extends southward along the coast of Brazil (De Oliveira et al., 1983). Other localities of this species are on the Atlantic coast of Africa, e.g. in Mauritania, Senegal, and Angola; it is expected that in future more locations will be discovered. It is remarkable that populations satisfying the diagnosis of this species have been found in Kenya. In southern Brazil the species is replaced by *H. emarginata*. Finally *H. beaudettei* occurs in the Gulf of Mexico, and less frequently in the Caribbean. It extends along the Atlantic coast of the USA northward up to North Carolina. This species has been found also along the Pacific coast, from Panama up to Mexico, where it reaches its northernmost locations in the Sea of Cortes. In the USA *H. beaudettei* is traditionally referred to as *H. wrightii*, but it relates in no way with the true *H. wrightii* which has been described after material from Cuba. The remaining two species are only known from one collection, *H. ciliata* from Pacific Panama, and *H. bermudensis* from the Bermuda Islands.

Although the identification characters show some variability at present no other means for identification are available. Studies of chromosome numbers, isozymes, and molecular analyses may be helpful to establish definitively the validity of the present species. The only chromosome count available, as far is known, suggests that possibly polyploidy is involved (den Hartog et al., 1979). McMillan (1980, 1982) found differences in the isozyme composition of East African and Texan *Halodule* populations, but provided no morphological descriptions of the used material.

Cymodocea König in König & Sims, Ann. Bot. 2 (1805) 96; nom. cons.
Type species: *Cymodocea aequorea* König (= *C. nodosa* (Ucria) Ascherson)

The genus, consisting of four species, has a mainly tropical distribution. *C. rotundata* and *C. serrulata* have a more or less similar pattern of distribution along the coasts of the tropical Indo-West Pacific. *C. nodosa* occurs in the subtropical Mediterranean and extends its area in the Atlantic northward to Portugal and southward to Senegal; further it is common on the Canary Islands. The fourth species, *C. angustata*, is endemic to the north-western part of Australia.

The distribution of this genus has been much wider in the past. In the Avon Park formation, a late Middle Eocene deposit in Florida, well preserved remains of seagrasses were found; among them were two species of *Cymodocea* (Lumbert et al., 1984). *C. floridana* differs from the present-day species, but is close to *C. angustata*. The second species appears to be preserved less completely; its leaf-blade is rather similar to that of *C. nodosa*. Fossil fruits have been found often in various deposits along the Mediterranean (Ruggieri, 1952). Another species, *C. micheloti,* has been recorded from the Miocene of Sulawesi (Celebes), Indonesia (Laurent and Laurent, 1926). This species is identical with the present-day *C. serrulata*.

Syringodium Kützing in Hohenacker, “Meeralgen” (Algae Marinae Exsiccatae) 9 (1860) no. 426
Type species: *Syringodium filiforme* Kütz.

This genus contains two species. *S. isoetifolium* is widely distributed in the coastal waters of the Indian Ocean and the western Pacific; along the west coast of Australia it penetrates far into the temperate zone and occurs even south of Perth. *S. filiforme* is restricted to the Gulf of Mexico and the Caribbean, and it has been recorded from Bermuda.

Thalassodendron den Hartog, Sea-grasses of the World (1970) 186
Type species: *Zostera ciliata* Forsskål (= *Thalassodendron ciliatum* (Forssk.) den Hartog)

This genus contains two species. *T. ciliatum* is widely distributed in the tropical Indo-West Pacific. In the Indian Ocean it is dominant on the reefs of the coasts of East Africa, many of the oceanic islands, and along the Red Sea. It does hardly occur along the northern coasts, as it absent from Pakistan, India, Sri Lanka, and BanglaDesh. In the western Pacific its occurrence is scattered, the northernmost locality being in the South Chinese Sea, the southernmost in Queensland. The other species, *T. pachyrhizum*, has a small area of distribution in the temperate south-western part of Western Australia, where it occurs on exposed reefs in the open ocean.

A fossil species, *T. auricula-leporis* has been described from the Middle Eocene Avon Park formation, Florida (Lumbert et al., 1984); its rhizome, however, does not show the regular features of the still living representatives of the genus; probably does it belong to an extinct genus of the Cymodoceaceae.

Amphibolis C. Agardh, Spec. Alg. 1 (1823) 474
Type species: *Amphibolis zosteraefolia* C. Agardh (= *A. antarctica* (Labill.) Sonder et Ascherson.

According to Ducker et al. (1977, p. 68) the genus *Amphibolis* was erected by C. Agardh (1823, p. 474) as a green alga with two species, *A. bicornis* (1823, p 474), and *A. zosteraefolia*, (1823, p. 475) from New Holland. Later, Agardh (1824, p. 192) recognized *A. zosteraefolia* as synonymous with *Ruppia antarctica* Labill., which was originally described by Labillardière (1806) as a flowering plant from the shore of Western Australia. Ducker et al. (1977) selected *A. zosteraefolia* instead of *A. bicornis* as the type of the *Amphibolis,* because, according to them, the type specimen of *A. zosteraefolia* has the unique grappling apparatus of which Agardh made the first description.

This genus is fully restricted to the temperate south and west coasts of Australia. It consists of two species. *A. antarctica* is distributed from Victoria and Tasmania in the east along the whole southern and western coast of Australia north to Carnarvon. The area of distribution of *A. griffithii* is more restricted; it occurs from Spencer Gulf in South Australia to the Geraldton area in Western Australia.

Posidoniaceae

Posidoniaceae Hutchinson, Fam. Fl. Pl. 2 (1934) 41; nom. cons.
Typus: *Posidonia* König

In earlier versions of the International Code of Botanical Nomenclature the name of the family has been ascribed to Lotsy (1911); he indeed used the name but did not add a formal description of the family.

Monoecious, perennial marine plants. Rhizome creeping, herbaceous, monopodial, with branched roots at the nodes; cortex with dark-colored secretory tannin cells. Scales covering the rhizome sheath-like, partly or completely amplexicaulous, scattered with fine brown dots (tannin). Erect lateral shoots ending in bundles of distichously arranged leaves. Leaf-sheath amplexicaulous or subamplexicaulous, biauriculate, ligulate. Leaf-blade linear with parallel nerves. Sheath as well as blade with numerous dark dots and stripes (tannin), the latter parallel with the nerves. Inflorescence cymose, pedunculate. Flowers hermaphrodite or masculine. Perianth absent. Stamens 3, sessile, consisting of a broad connective with at each side an extrorsely dehiscent, bilocular theca. Pollen confervoid. Gynoecium containing one orthotropous, parietal, pendulous ovule. Stigma irregularly lobed. Fruit with fleshy pericarp. Seed filled completely by the embryo; embryo straight, consisting for the greater part of a large, fleshy hypocotyl with an apical 4-polyphyllous plumula. Hypocotyl with numerous tannin cells. Primary root present or absent.

The family contains only the genus *Posidonia*, the history of which goes back to the Cretaceous.

Posidonia König in König & Sims, Ann. Bot. 2 (1805) 95; nom. cons.
Type species: *Posidonia caulini* König (= *P. oceanica* (L.) Delile)

The genus *Posidonia* has a rather remarkable pattern of distribution; one species, *P. oceanica*, is completely restricted to the Mediterranean; the other eight species of the genus occur in the waters of temperate Australia (Cambridge and Kuo, 1979; Kuo and Cambridge, 1984). Although there is no need to split the genus into sections or subgenera three groups can be recognized. *P. oceanica* forms a group in itself, because of the development of a significant primary root from the embryo. In the Australian species there is no development of a primary root at all. Among them two groups can be distinguished.

P. australis, *P. angustifolia*, and *P. sinuosa* form together the *P. australis*-group (Cambridge and Kuo, 1979). These species are found in relatively sheltered coastal waters where they can form extensive monospecific beds. They have thin, rather flexible, short leaves, relatively large air lacunae and rather few fibre bundles; their roots are rather fine and much branched. Their leaf-sheaths are short, so the meristems are not very deeply buried.

In contrast the five species of the *P. ostenfeldii*-group (*P. ostenfeldii, P. robertsoniae, P. denhartogii, P. coriacea*, and *P. kirkmanii*) grow in the open ocean and in high energy coastal sublittoral habitats (Kuo and Cambridge, 1984). They are characterized by very long, thick, tough, leathery leaves, with narrow air lacunae and an abundance of fibre bundles in the subepidermal layer and in the mesophyll. The leaf-sheaths are very long, up to 25 cm, and the meristems are deeply buried in the substrate (20–30 cm); the roots are very long and sparsely branched, showing wrinkled expanded thickenings up to 3 mm thick.

Recently, Campey et al. (2000) re-evaluated the species boundaries of the members of the *P. ostenfeldii* species complex in one locality, and found that there is a continuous variation of the character traits within the complex, suggesting the existence of a morphological continuum between the species; they also did not find any allozyme variation. According to them *P. coriacea* and *P. robertsoniae* are not separate species, and have to be regarded as synonyms.

Hydrocharitaceae

Hydrocharitaceae Juss., Gen. Pl. (1789) 67; nom. cons.: pro parte (excluding the dicotyledons *Nymphaea*, *Nelumbio*, *Trapa, Proserpinaca*, and the monocotyledon *Pistia* which were included in the original description of the family).
Typus: *Hydrocharis* L.

Monoecious or dioecious, annual or perennial aquatic plants, having either a creeping monopodial rhizome with unbranched roots at the nodes, and distichously, rarely tristichously, arranged leaves, or an erect main axis (which may be highly contracted) with roots at the base, and spirally arranged or verticillate leaves. Leaves submerged, sometimes floating or partly emerged, linear, lanceolate, elliptic, ovate or orbicular, either sessile and then sometimes sheathing at the base, or differentiated into a leaf-blade and a petiole, always without a ligula; nerves more or less parallel, straight or curved, connected by perpendicular or ascending cross-veins. Stipulae sometimes present. Squamulae intravaginales present. Flowers actinomorphous or, rarely, slightly zygomorphous (*Vallisneria*), with a true, trimerous perianth, unisexual, and then sometimes with rudiments of the other sex, or bisexual, sessile or pedicellate, solitary or arranged in a cymose inflorescence, enclosed by a spathe. Spathe consisting of two free or partly to completely connate spathal leaves (bracts), pedunculate or sessile. Perianth consisting of 1 or 2 whorls of 3 segments. Stamens (2-) 3-several, arranged in one or more whorls; anthers basifixed, bi- or quadrilocular, longitudinally dehiscent; filaments more or less slender, sometimes absent. Pollen globose, sometimes released in moniliform chains (*Halophila, Thalassia*). Gynaecium paracarpous. Ovary inferior, linear, ellipsoid or ovoid, consisting of (2-) 3-15 carpels, unilocular; between ovary and perianth often a long, filiform hypanthium. Placentas parietal either protruding nearly to the centre of the ovary, or obsolete. Styles (2-) 3-15, often more or less split into two stigmatic branches. Ovules several, orthotropous to anatropous, erect or pendulous, with two integuments. Fruits indehiscent, opening by decay of the fleshy or membranous pericarp; or, rarely stellately dehiscent (*Thalassia*). Seeds several, fusiform, ellipsoid, ovoid or globose. Embryo straight, either with the hypocotyl and the cotyledon not distinctly separated and with a very inconspicuous plumula at the base of a lateral groove; or with a well differentiated hypocotyl and cotyledon and a large well developed plumula. No endosperm.

The family contains 17 genera, of which *Thalassia*, *Halophila*, and *Enhalus* are fully marine.

Thalassia as well as *Halophila* have been regarded to be sufficiently different from a morphological point of view to erect special subfamilies for them; some authors considered them even as separate families. Nakai (1943), for example, erected the family Thalassiaceae for the genus *Thalassia*, because of its ‘confervoid’ pollen (in fact strings of spherical pollen), its distichous linear leaves, its quadrilocular, laterally dehiscent anthers, and its superior ovary (an incorrect observation as the ovary is inferior). Nakai (1943) erected also the family Halophilaceae to contain the genus *Halophila*, because of its ‘confervoid’ pollen (strings of pollen as in *Thalassia*), its opposite, stipulate, petiolate, pinnately nerved leaves, its bilocular extrorse anthers, and its inferior ovary. In our opinion the family status is not really warranted for these genera; the subfamily status within the Hydrocharitaceae expresses in fact sufficiently the special position as well as the relationship of these taxa.

The status of a possible arrangement of the remaining 15 genera within subfamilies is still open to debate. Ascherson and Gürke (1889) and Eckardt (1964) distinguished two, Dandy in Hutchinson (1934) only one, and Dahlgren et al. (1985) three subfamilies, while Tomlinson (1982) refrains from giving an opinion on this subject. Cook (1998) does not arrive at a formal classification, but distinguishes three groups, (1) the *Limnobium*-group, (2) the *Vallisneria*-group, and (3) the *Elodea*-group and the more or less alone standing genus *Blyxa*, that according to him could be considered to represent the archetype of the family. Cook places the seagrass *Enhalus* in the *Vallisneria*-group, but according to him, in spite of the reductions in many morphological and anatomical characteristics, it shows features that indicate intimate affinities to the *Limnobium*-group. Nakai (1943) regarded *Enhalus* as representing a family on its own, the Enhalaceae, mainly because it is a 'planta maritima'; this family is untenable, but unfortunately validly published in accordance with the rules of botanical nomenclature. On morphological grounds the seagrass *Enhalus* seems to be clearly related to the fresh-water genus *Vallisneria*, and has been classified by den Hartog (1970) within the subfamily **Vallisnerioideae**. Les et al. (1997) suggest another arrangement of the Hydrocharitaceae based on the *rbc*L gene sequence. Independent molecular research by Tanaka et al. (1997) using the *rbc*L and *mat* K gene sequences indicates that *Najas*, generally classified as a family of its own (Najadaceae), is an in-group of the Hydrocharitaceae, and thus would lose its special status. Further, they demonstrated that the three marine genera, *Enhalus, Halophila*, and *Thalassia* form a monophyletic grouping, but the recognition of all marine Hydrocharitaceae as a separate monophyletic family is not strongly supported by the *rbc*L data. Therefore, Les et al. (1997) concluded that these genera must be retained as a single taxon, e.g. as a subfamily, within the Hydrocharitaceae rather than as a distinct marine family. In our opinion the three marine genera have in common that they fit the morphological basic plan of the Hydrocharitaceae and possess a set of physiological properties to deal with life in the marine environment. Apart from these basic characters the three marine genera show hardly any similarities. The molecular data probably indicate that the adaptation to the marine conditions in the three genera has followed a similar pattern and that probably the same physiological mechanisms are involved. For this reason we keep to the view that the two marine subfamilies **Thalassioideae** and **Halophiloideae** should be maintained and that *Enhalus* belongs to the **Vallisnerioideae**.

Key to the Marine Genera

1a. Very coarse plants with a thick rhizome and strap-shaped leaves; leaf margins with very coarse nerves, after decay remaining as persistent strands. Flowers with three petals and three sepals. Male spathe with numerous flower-buds which become detached just before flowering, the flower then floating freely at the water surface. Pollen spherical, free. Female flower on a long peduncle, which spirally contracts after pollination. Tannin cells present ..... ***Enhalus***

1b. Moderately coarse or even very delicate plants with more slender rhizomes. Male spathe containing only one flower, shed after anthesis. Pollen spherical, arranged into moniliform strings. Tannin cells present or absent.

2a. Leaf-bearing branches arising from the rhizome at distances of several internodes; each internode covered by a scale. Leaves distichous, linear; nerves parallel. Spathal leaves partly connate. Styles 6–8, each divided into two stigmata. Parietal placentas protruding far into the centre of the ovary. Fruit stellately dehiscent. Tannin cells present .... ***Thalassia***

2b. Leaf-bearing branches arising from the thin rhizome at each node. Leaves petiolate, in pairs, in pseudo-whorls or distichously arranged; with a pinnate nervation. Spathal leaves free. Styles 3–6, not divided. Parietal placentas protruding only slightly into the ovary. Fruit dehiscent by decay of pericarp. Tannin cells absent .... ***Halophila***

Enhalus L.C. Richard, Mém. Inst. Paris 12, 2 (1812) 64,71,74.
Type species: *Enhalus koenigi* Rich. (= *E. acoroides* (L. *f*.) Royle)

Enhalus is a monotypic genus, widely distributed along the coasts of the Indian Ocean and the tropical part of the western Pacific.

Thalassia Banks ex König in König and Sims, Ann Bot. 2 (1805) 96
Type species: *Thalassia testudinum* Banks ex König

This genus contains two well-defined species. *T. hemprichii* is widely distributed in the coastal waters of the Indian Ocean and the western Pacific. *T. testudinum* is restricted to the Gulf of Mexico and the Caribbean, and it has been recorded from Bermuda.

Fossil leaf material of *T. testudinum* has been found in the Avon Park deposits from the Middle Eocene of Florida (Lumbert et al., 1984).

Halophila Du Petit Thouars, Gen. Nov. Madag. 2 (1806) 2
Type species: *Halophila madagascariensis* Steudel, validated by Doty & Stone, 1967.

The typification of *Halophila* has been a weary affair, because the original author of the genus did not describe the species on which the genus was based. Steudel (1840, p. 515) published the name *H. madagascariensis* without a description of the species, thus not validly, but the geographical indication makes it clear that he must have referred to the material of Thouars; at that time there were no other collections of *Halophila* from Madagascar in the Paris herbarium. Doty and Stone (1967) validated the name after 127 years. In 1970 den Hartog considered this species still as a synonym of *H. ovalis*, which is based on *Caulinia ovalis* from Australia (K, BM), and did not give *H. madagascariensis* even the status of a subspecies. After a new study we now agree that the two taxa indeed show some differences. There is, however, another option for the typification of the genus, as *H. ovata* was the first species described and illustrated within the genus.

In the genus *Halophila* five sections have been described, based on differences in the gross vegetative morphology of the plants. These sections do not show differences with respect to the structure of the flowers; the variation in the number of styles, for example, may differ between populations of the same species. Differences in the way of arrangement of the flowers into inflorescences seem more characteristic at the species level; the same holds for monoecy and dioecy.

Most species can be classified within the typical section, *Halophila* sect. *Halophila*. This section contains all *Halophila* species with one pair of petiolate leaves born on short erect lateral shoots. It is the morphologically most diverse group and its geographical distribution coincides with that of the whole genus. The species of this section occur in various habitats and show a large morphological variability; some of these variants can be treated as independent taxa in their own right. Currently, there are ten described species: *Halophila ovalis* (consisting of four subspecies), *H. madagascariensis, H. ovata, H. minor, H. australis, H. johnsonii, H. decipiens, H. capricorni, H. stipulacea,* and *H. hawaiiana.* These species and the subspecies of *H. ovalis* have recently been briefly redescribed, with the exception of *H. madagascariensis* (Kuo and den Hartog 2001).

Most of the species of the section *Halophila* are restricted in their occurrence. Only *H. decipiens* is widely distributed occurring in both the northern and the southern hemisphere, along the tropical and subtropical coasts of the Indian, the Pacific, and the Atlantic Oceans, but the species has not been recorded so far from the Mediterranean.

H. ovalis is widely distributed in the tropical Indo-West Pacific and penetrates in some areas beyond the tropics, e.g. in Western Australia, and in Japan as indicated by Miki (1934). *H. minor* has also a wide area of distribution, from East Africa to the western Pacific, but it does not extend beyond the tropics. *H. stipulacea*, is very common along the eastern coasts of Africa, in the Red Sea and the Persian Gulf, and also occurs on Madagascar and along the west coast of India. This species has invaded the Mediterranean via the Suez Canal and is there still expanding its area of distribution (Den Hartog, unpublished). *H. australis* has a wide distribution in the temperate seas of southern Australia, *H. capricorni* is restricted to the Coral Sea, and *H. ovata* occurs only in the northern part of the western Pacific (Saipan, Guam, Yap, Manila Bay) (Kuo 2000). *H. johnsonii* is the rarest species as it is restricted to one area in Florida.

It appears that various morphologically distinct species in this section could not be distinguished by a recent molecular study (Waycott et al. 2002). McDermid et al. (2003) reported that several morphological variations with little genetic variation occur in populations of *H. hawaiiana* from different islands of the Hawaiian Archipelago. Procaccini et al. (1999b) found that the recently established populations of *H. stipulacea* on Sicily exhibited both significant morphological variations with depth and site as well as high genetic polymorphism, but these variations appeared to show no correlation. These authors suggested that this phenomenon might be influenced by environmental conditions and through vegetative or other means of asexual reproduction; however, they did not specify which environmental factors and did not make an effort for collecting or observing reproductive materials from different populations.

The section *Spinulosae* Ostenfeld is characterized by having much elongated, stiff erect lateral shoots bearing up to 20 pairs of distichously arranged sessile leaves at the nodes. The section consists of only one species, *H. spinulosa*, which is morphologically fairly homogeneous. Japar Sidik et al. (2000) reported, however, that there are some populations in Malaysia where the leaves are tristichously arranged. The species is common in Malaya, and extends via Indonesia where it is rare, to New Guinea and tropical and subtropical Australia. There are no records of the species from Thailand and Vietnam; the most northern record is from Luzon, Philippines.

The section *Microhalophila* Aschers. is characterized by the possession of distinct erect lateral shoots, which bear on the top a pseudo-whorl of 4–10 sheathing petiolate leaves. It contains one delicate species, *H. beccarii*, which shows some slight morphological variation. This species is widely distributed along the southern shores of the South Chinese Sea, the Gulf of Thailand, the Gulf of Bengal, and the Indian coast of the Arabian Sea. So far, it has not been recorded from Indonesia and Australia. It reaches its northern limit in south China and Taiwan. The species is usually associated with mud flats and mangrove communities and often exposed at low tide.

The fourth section of the genus, sect. *Americanae* Ostenfeld is characterized by having distinct erect lateral shoots with two scales about half way up and a pseudo-whorl of 4–8 leaves at the top. It contains two morphologically fairly distinct dioecious species, *H. engelmanni*, which occurs in the Gulf of Mexico and the northern Caribbean (Cuba), and *H. baillonii*, which has been recorded from the southern Caribbean, the Pacific coast of Central America, and from Brazil.

The fifth section of the genus, sect. *Tricostatae* Greenway, consists of fragile plants with herbaceous, elongated erect lateral shoots bearing at each node a rosette of (2-) 3 leaves. The section contains only one annual, dioecious species, *H. tricostata,* which is restricted in its occurrence to north-eastern Australia.

Ruppiaceae

Ruppiaceae Horaninov, Prim. Lin. Syst. Nat. (1834) 46; nom. cons.
Typus: *Ruppia* L.

In earlier editions of the International Code of Botanical Nomenclature the name of the family was ascribed to 'Horaninov ex Hutchinson, Fam. Fl. Pl.2 (1934) 48'.

Monoecious, annual or perennial submerged aquatic herbs. Rhizomes creeping, monopodial, but often also laterally branched; in annual species often considerably reduced. Central cylinder with a vascular strand, with in the centre a xylem canal; cortex consisting of parenchyma with a circle of air channels. From each node 1 or 2 unbranched roots with numerous very fine root-hairs arise, as well as an erect shoot. Shoots very short to up to more than 2.5 m high, in the latter case profusely branched. Internodes elongate, variable in length. Leaves linear, distichous, with very many tannin cells; leaf-sheath amplexicaulous, with on either side a slightly auriculate membranous flap; flaps overlapping; no ligule; leaf-blade with only a midrib; margins smooth, but near the leaf-tip irregularly serrulate; on either side of the midrib a wide air lacuna. Uppermost leaves of generative branches opposite.

Inflorescence terminal, consisting of a peduncle, which has at its top a two-flowered spike. Peduncle arising from between the inflated sheathing bases of the two apical leaves; short, erect and sometimes thickened after flowering, or thin and varying in length from a few cm to more than a metre (often still lengthening itself by cell stretching during the flowering process), and in most of the species after flowering coiled or spirally contracted, pulling the ripening fruits down to the bottom. Flowering takes place at the water surface, or submerged. Flowers placed at opposite sides of the axis, but very closely together, bisexual, without a perianth, consisting of two opposite stamens and 4-numerous carpels. Stamens consisting of one (sub-)sessile, bilocular anther; connective broad with at each side a theca; thecae circular to broad-elliptic, extrorsely dehiscent, shed after emission of pollen. Pollen boomerang-shaped with reticulate exine. Pollination aerial, on the water surface, or under water in an air bubble. Carpels free, sessile or subsessile; ovary ovoid; no style, but a small peltate disc-like stigma. In most species a podogyne develops at the base of each carpel after fertilization, giving the infructescence an umbellate appearance. Ovule solitary, pendulous, campylotropous. Fruit an achene, sessile or stalked (podogyne and fruit form a morphological entity without abscission zone), symmetric to very asymmetric; exocarp spongy, soon decomposing; endocarp hard, persistent with beak and usually a podogyne; at the apical part of the endocarp a small foramen occurs, the shape of which has diagnostic value at the species level.

The family contains only one genus, *Ruppia*.

Ruppia L. Sp. Pl. (1753) 127.
Type species: *Ruppia maritima* L.

Widely distributed in temperate and tropical regions all over the world, in the northern hemisphere even extending beyond the polar circle, and from sea level up to 4000 m altitude. The greatest species diversity seems to occur in mediterranean-type climates, in poikilohaline environments. It occurs in brackish waters as well as in continental salt waters, but also in highly diluted fresh waters and in hyperhaline waters where it tolerates salinities up to three times the salinity of the sea. It has also been found under marine conditions, but only in very sheltered places, where also very large temperature fluctuations may occur. Its occurrence in the tropics is very local, probably because the environments where representatives of this genus would abound are ephemeral under tropical conditions. Lagoons, which become detached from the sea, will be brackish only very temporarily; in the wet tropics they will develop into freshwater marshes due to dilution with rain, and in the dry tropics they will become desiccated and transformed into a salty desert.

Circa 10 species are known. As a consequence of the great morphological variation between populations, partly due to environmental differences and partly genetically determined, the taxonomy of the genus is still unsatisfactory. Another difficulty is that in the past it was not recognized that in the herbarium material the flowering and fruiting organs were not always in the same stage, so the number of described varieties is large; most of them cannot be maintained. However, many investigators have concluded from the chaotic taxonomic situation that the best solution to the problem was to consider the genus as containing one very variable species. This has given cause to the uncritical 'traditional' identification of specimens of this genus as *R. maritima*. Studies based on the investigation of living plants, herbarium material and chromosome analyses in Europe (Reese, 1962; Verhoeven, 1979), Australia (Jacobs and Brock, 1982) and New Zealand (Mason, 1967) have shown that this is not correct. It is obvious that the genus is in an urgent need of revision on a world scale. This revision should not only be based on herbarium material, but also on the study of living material cultured under various ecological circumstances; further chromosome and isozyme studies should be included.

The genus *Ruppia* has been classified in the past in various ways; several authors considered it as a family on its own, the Ruppiaceae, but it has also been regarded as a subfamily of the Potamogetonaceae. According to Jacobs and Brock (1982) the differences with *Potamogeton* are not sufficient to warrant a separate position within the Potamogetonaceae *sensu stricto*. Les et al. (1997) have shown that molecular *rbc*L data indicate that *Ruppia* is phylogenetically much closer to *Posidonia* than to *Potamogeton*.

The only exclusively marine species of the genus has not yet been formally described, and is indicated as *R*. aff. *tuberosa* (den Hartog, in preparation)

Zannichelliaceae

Zannichelliaceae Dumortier, Anal. Fam. Pl. (1829) 59, 61; nom. cons.
Typus: *Zannichellia* L.

Monocious or dioecious, annual or rarely perennial aquatic herbs. Rhizome creeping, sympodial, often poorly developed, herbaceous, rooting at the nodes. Roots not branched, 1-several per node. Scales on the rhizome membranous, caducous. Erect shoots arising from each node, sympodial, branching profusely and producing flowers arranged in a rather complex inflorescence. Leaves distichously arranged, sometimes alternate or in a pseudo-whorl, linear, green, without tannin cells, with a single central vein, on each side of it with 1–2 parallel air channels; margin entire; leaves with a ligule, sheathing at the base, or without a ligule, but with free stipules at the base of the leaves (*Zannichellia*). Tannin cells absent. Flowers terminal. Male flower with or without perianth, with one stamen consisting of 2–12 longitudinally dehiscent, sporangiate cells, with or without connective appendages. Stamens generally submerged, but in at least one species emerging above the water surface. Pollen spherical. Female flower consisting of a cup-shaped structure, the cupula, with 1–8 sessile or shortly pedicellate free carpels. Cupula consisting of three tepals, which are free (*Lepilaena, Althenia*), or united to form a closed tube (*Zannichellia, Pseudalthenia*). Carpels with a short (*Zannichellia, Pseudalthenia*) or a long style (*Lepilaena, Althenia*); stigma funnel-shaped or peltate with a smooth, lobate, or feathery appearance. Ovule 1, anatropous, pendulous. Fruit an achene, with a hard endocarp, a soft mesocarp and a membranous exocarp, and a terminal beak. In some species a short podogynium is developed after fertilization, forming an integral part of the fruit without an abscission zone. Fruit wall smooth or tuberculate. No endosperm.

The family has a world wide distribution, and consists of four genera. The taxonomy of the family at the genus level has been worked out by Tomlinson and Posluszny (1976). *Zannichellia* has a very wide distribution, almost covering the area of the family, and has been recorded from sea level up to the high Andes and the Himalayas. The species of this genus occur in brackish as well as hard fresh water, in standing ponds and lakes as well as in streams, but do not inhabit marine sites. Most of these species are also tolerant to large temperature fluctuations, and their seeds can stand protracted desiccation. In the past the genus has been considered to consist of one extremely variable species, *Z. palustris*. This has often led to an uncritical 'traditional' identification of plant material of this genus. It has, however, turned out that a number of well-defined species can be recognized. In Europe at least six species occur (Van Vierssen, 1982; Van Vierssen and Van Wijk, 1982; Uotila et al., 1983; Talavera et al., 1986), and more species are expected to be recognized, as the material from the Ponto-Caspian area and Central Asia has been subjected to a critical study. Haynes and Holm-Nielsen (1987) described a species from the Andes. The genus is urgently in need of a revision. *Althenia*, with one or two, but possibly more species, is distributed from the Mediterranean area to Central Asia, and has further been recorded from South Africa. It occurs in saline waters of salt marshes along the coast, but is also widely distributed in continental salt waters. The genus *Pseudalthenia* (also known under the name *Vleisia*) is monotypic and is restricted in its occurrence to a few brackish-water environments in the Cape Province of South Africa. *Lepilaena* is the only genus in this family with a true marine species.

Lepilaena Drummond ex Harvey, J. Bot. Kew Gard. Misc. 7 (1855) 57
Type species: *Lepilaena australis* Drummond ex Harvey

The genus contains at least six species which all are widely distributed in temperate Australia; one of these, *L. bilocularis*, is shared with New Zealand. Robertson (1986) gives a key to the presently described species of the genus. Its representatives occur in all kinds of brackish water habitats, but also in continental salt waters; further they inhabit hard fresh water environments such as shallow lakes and ponds, and are often found in temporary pools. A still undescribed species has been collected in a shallow temporary soft water environment in south-western Australia. One species, *L. marina*, has been found so far only in sheltered marine environments; in vegetative condition this species can be confused with *L. bilocularis*. Marine records of the latter almost certainly refer to *L. marina*, e.g. the records by den Hartog (1970).

IV. Biogeography

The first attempt to analyze the geographical distribution of the seagrasses was by Ascherson (1871), who produced also the first world map of their distribution. At present this paper has only historical value, as taxonomy of the seagrasses and knowledge of their distribution has increased enormously since, not least by the continuous efforts of Ascherson himself to obtain material from all over the world, and to publish updates (Ascherson, 1875, 1906). His work has been continued by the publication of the fine essays by Ostenfeld (1915) and Setchell (1920, 1935). Ostenfeld published also a number of detailed maps of the areas of distribution of the seagrass species known at that time in the prestigious series 'Pflanzenareale' (Ostenfeld, 1927a, marine Hydrocharitaceae; 1927b, marine Potamogetonaceae, i.e. representatives of the Zosteraceae, Posidoniaceae and Cymodoceaceae). In his monograph den Hartog (1970) described the areas of all known species, based on the collections available at that time, and produced maps of the distribution of all 12 genera. These maps show also perfectly that the pattern of seagrass distribution, already suggested by Ascherson (1906), has become more and more prominent. Later publications show a further increase in knowledge; Lüning (1990, p. 204) amended the genus maps of den Hartog. Larkum and den Hartog (1989) discussed the evolution of seagrass genera and events that gave rise to their current distribution. Regrettably the species maps given by Green and Short (2003) in their world atlas of seagrasses (2003 Appendix 3) are not always fully accurate.

Seven genera appear to be mainly distributed along tropical coasts, viz. *Thalassia*, *Halophila*, *Syringodium*, *Halodule*, *Cymodocea*, *Thalassodendron* and *Enhalus*. The first four genera have representatives in the tropical Atlantic as well as in the Indo-Pacific. The other three genera are restricted to the Indo-West Pacific. However, with respect to *Cymodocea, Halophila* and *Thalassodendron* the picture is somewhat more complicated. One of the *Cymodocea* species, *C. nodosa*, has a more warm-temperate distribution in the Mediterranean, and fans out into the Atlantic along the Iberian Peninsula and the north-western coast of Africa where it just passes the Tropic of Cancer. *Halophila*, with 15 described species the most species-rich genus of the seagrasses, has developed a warm-temperate species, *H. australis*, occurring along the southern shores of Australia, and the widespread Indo-West Pacific species, *H. ovalis*, extends its area in East Asia far beyond the tropics. *Thalassodendron* has one species with a wide distribution in the tropical Indo-West-Pacific and a second species with a very small area of distribution along the warm-temperate south-western coast of Australia. In all other cases where tropical species cross the Tropic of Cancer (e.g. in the northern Red Sea, and the Ryukyu Islands) or the Tropic of Capricorn (*Syringodium isoetifolium* along the Australian West coast) warm currents make this possible. It is striking that the tropical Atlantic seagrass flora has no genera of its own, although it is well distinguished at the species level. The only supraspecific taxon characteristic for the tropical Atlantic, with one outlying record for Pacific Central America (den Hartog, 1960), is *Halophila* sect. *Americanae*.

Five genera are mainly distributed along the world's temperate shores, viz. *Zostera*, *Phyllospadix*, *Heterozostera*, *Posidonia* and *Amphibolis*. Two of these genera have their distribution in the northern as well as in the southern hemisphere. *Zostera* subgen. *Zosterella* has representatives in temperate Australia, New Zealand, southern Africa, as well as in eastern Asia and along the Atlantic and Mediterranean coasts of Europe, and northern Africa. *Z. noltii* is the only species occurring in the continental relict seas of western Asia (Caspian Sea and Aral Sea). It is striking that up to very recently this subgenus has been absent from the Atlantic as well as the Pacific coasts of the Americas. *Zostera* subgen. *Zostera* is restricted to the northern Pacific and the northern Atlantic, and also occurs in the Mediterranean and the Black Sea. *Posidonia* is the second genus with a bipolar distribution, but in contrast to *Zostera* the northern hemisphere distribution is restricted to one species in the Mediterranean, and in the southern hemisphere it occurs with eight species in Australia. *Heterozostera* and *Amphibolis* are restricted to temperate Australia, apart from a small area occupied by the endemic *H. chilensis* in Chile. Only some species of *Zostera* subgen. *Zosterella* penetrate here and there within the tropics.

The Arctic Sea has no species of its own, although the cold temperate species *Zostera marina* crosses the Arctic Circle in Europe as well in the northern Pacific. Antarctica is devoid of seagrasses.

In spite of shipping, fishing, culturing marine organisms, and other human activities over the centuries, the areas of distribution of the seagrasses are still reasonably intact. The only changes which are of an anthropogenous nature relate to *Z. japonica* which has been accidentally introduced in Pacific North America and is still expanding its area (Harrison, 1976; Bigley and Barreca, 1982), and *Halophila stipulacea* which has passed through the Suez Canal and has conquered the eastern Mediterranean. Of course, within the known areas large changes in abundance of species have taken place, of which many are indicated in the atlas of Green and Short (2003).

In the reviews by Larkum and den Hartog (1989) and Kuo and den Hartog (2000) it is already stated that the origin of the seagrasses is still very unclear. Fossil material is extremely rare. Most of the fossils thought to be seagrass appeared not to be seagrass at all. The original material of *Archeozostera*, described from the Cretaceous of Japan, appeared after a profound study by Kuo et al. (1989) not to be a seagrass and probably not even a plant. There was already some doubt about *Thalassocharis*, described from the Cretaceous of Westfalen (Germany) and Maastricht (The Netherlands), as the stems had no seagrass morphology; the absence of air lacunae leads to the conclusion that it is not an aquatic plant. The only seagrass genus of which the Cretaceous origin can be confirmed appears to be *Posidonia*. *P. cretacea* Hos. et v. d. Mark, described from Germany, is not very well known, but recently a very fine specimen, consisting of a bundle of leaf-sheaths fully comparable with the 'shaving brush' of the mediterranean *P. oceanica*, has been collected from the Cretaceous of Maastricht.

Other seagrass fossils are known from the Eocene of the Basin of Paris; these have been assigned to *Posidonia parisiensis* (Brongt.) Fritel, *Cymodocea serrulata* and *C. nodosa* (den Hartog. 1970; Larkum and den Hartog, 1989). An other set of Eocene seagrass fossils has been collected from the Avon Park formation in Florida, viz. *Thalassodendron auricula-leporis* den Hartog, *Cymodocea floridana* den Hartog and *Thalassia testudinum* (Lumbert et al. 1984). It is remarkable that most of these Eocene fossils can be identified as, or are morphologically very similar to, presently still extant species. *C. floridana* shows a striking resemblance to *C. angustata*, which has a very small area of distribution in northwestern Australia (Kuo and den Hartog, 2000). The Eocenous *Thalassodendron* species is rather different from the modern species, and may be classified into a genus of its own. Beautifully preserved fossils of *C. serrulata* have been collected from the Miocene of Sulawesi (formerly Celebes) as *C. micheloti* (Laurent and Laurent, 1926).

From these few confirmed fossils it can be concluded that seagrasses already developed at an early stage of the evolution of the angiosperms. Taking into consideration that at present three exclusive seagrass families can be recognized, and a fourth family with two seagrass subfamilies, the possibility may not be excluded that the evolutionary transition from terrestrial plants to fully submersed marine plants may have taken place just as many times. Les et al. (1997) concluded after a phylogenetic analysis that among the seagrasses three lineages can be recognized giving evidence that these lineages independently entered the marine environment. These lineages are (i) the Zosteraceae, (ii) the Cymodoceaceae complex consisting of the Posidoniaceae, the Cymodoceaceae and the Ruppiaceae, and (iii) the Hydrocharitaceae.

The Ruppiaceae and the Zannichelliaceae occur in waters with a very diverse chemical composition, such as brackish and continental salt waters, but also in hard fresh waters. *Ruppia* species sometimes occur in the marine environment, particularly in the intertidal zone of muddy or sandy flats where seagrasses are absent; after the introduction of *Zostera japonica* in North America *Ruppia* decreased markedly. In temperate Australia *Lepilaena* (Zannichelliaceae) occurs with *Ruppia* in brackish waters. Both genera have developed one species that is fully restricted to very sheltered marine conditions, and these two species generally form together a community. These species are probably the most recent seagrasses in the evolutionary history.

It is apparent from the very limited fossil record that the distribution of the seagrasses must have been quite different from the present situation, as is demonstrated by the fossil occurrence of *Cymodocea* and a *Thalassodendron*-like species in North America, genera presently absent from America.

Another fact is that fossil material of Zosteraceae has not been found in Cretaceous or Tertiary deposits, but only in Quaternary layers; the presence of *Z. noltii* in the Caspian and Aral Seas shows, however, that on the ground of the history of these seas *Zostera* must have been in existence already in the Miocene. Larkum and den Hartog (1989) have attempted to use all kinds of geological data to work out the history of the Australian seagrass flora. The great handicap for this approach remains the lack of fossil material. Of the 12 presently living seagrass genera some fossil remains of only four are known, and this is insufficient to elaborate in a reliable way the areas of origin of the various families. One would expect that thick seagrass deposits, as presently known from *Posidonia* species and *Thalassodendron ciliatum*, must have been formed also in the past. Therefore, it is recommended that seagrass researchers should more cooperate with paleontologists when marine geological deposits are explored.

V. Conclusion and Outlook

We acknowledge the important contribution made by molecular technology [*rbc*L, *mat*K (plastid DNA) and ITS (nuclear DNA) gene sequences] in our understanding of phylogenetic relationships of seagrasses, particularly at the higher levels for which this approach has been developed (the reader is referred to Waycott et al., Chapter 2, for an in-depth review of this topic). However, this powerful tool may not always be suitable for defining the species and cannot replace the morphological characters generally used for species identification. To consider taxa which cannot be separated by the present molecular techniques as ‘phenotypic plasticity’ of a wider molecularly defined ‘biological species’ is not really a solution of the problem; new advanced techniques may show that they are indeed different. There is a great need to correlate the molecular data to morphological and physiological data.

In this connection we refer to the works of McMillan, who studied isozymes (McMillan, 1980, 1982, 1991; McMillan and Williams, 1980) and sulfated flavonoids (McMillan et al., 1980; McMillan, 1983, 1986) in many seagrass species, but he generally did not give morphological descriptions of the material used, with the exception of the taxa within the genus *Halophila*. In the latter case the isozyme and flavone patterns seem characteristic at the species level, but unfortunately the number of observations is low. More research is necessary, as McMillan and Williams (1980) clearly state.

Admittedly the number of useful morphological characters that can be used to identify the seagrass species is very limited due to the relatively simple morphological and anatomical features in both the vegetative and the reproductive organs of seagrasses; this holds in fact for many other aquatic plants as well (see Chapter 3, Kuo and den Hartog). So, another powerful tool, that of the cladistic analysis, which often is employed in terrestrial plant taxonomy may not be very suitable for seagrass taxonomy, as demonstrated by Les et al. (2002).

It is true that the currently available knowledge of seagrass taxonomy, in particular where the definition of species is concerned, is not always adequate and requires an urgent improvement. Basic morphological and anatomical studies on as many samples as possible from wide geographic areas and growing under as many different habitat conditions as possible should be conducted. It is very important that good documentation of morphological and anatomical variations within the species from the various study areas becomes available; it has to be encouraged that samples of material used for molecular, physiological, phytochemical and morphological research are deposited in the recognized herbaria for future study and to improve the descriptions of species. Without such fundamental studies, the queries on identification of variable species such as those of *Zostera, Halodule,* and *Halophila* will continue to persist. A stable taxonomy is a necessary base for all botanical research. Therefore, it is also recommended that, if possible, type material of the various taxa is included in the analyses.

Finally we have come to the conclusion, in agreement with Tomlinson (1982), that there are no special morphological characters that distinguish the seagrasses from other aquatic plants. The only character in which most of them differ from the other aquatic plants is the filiform pollen (Zosteraceae, Posidoniaceae, Cymodoceaceae) or the strings of spherical pollen (*Thalassia, Halophila*); however, we do not see what the special advantage of these may be for life in the marine environment.

The seagrasses as well as the aquatics of the eurysaline group, obviously, differ from the other aquatic plants by their ability to live in waters with a high salinity. It is at present still not clear how they cope with this situation. The fact that the seagrasses inhabit generally the homoiohaline waters, where the environmental conditions are relatively stable, and the eurysaline species the poililosaline waters where they are generally subjected to large fluctuations in salinity, indicates that these plants must have evolved very special physiological mechanisms to deal with these problems. So far very little is known about these mechanisms; it is not even clear whether there is only one mechanism or whether each family involved has developed its own way to deal with salinity, as the families are not closely related. These mechanisms are certainly firmly fixed in the genomes of these plants. Therefore, we recommend a thorough study of the physiology of both the seagrasses and the eurysaline aquatics in order to solve this basic problem.

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Appendix: A List of the Seagrass Species of the World

The list presents all taxa recognised as seagrasses. Eurysaline taxa which may be found in brackish water and occasionally under marine conditions have not been incorporated.

Zosteraceae

1. Zostera Linnaeus

Zostera subgenus **Zostera**

1. *Zostera marina* Linnaeus
2. *Zostera caespitosa* Miki
3. *Zostera caulescens* Miki
4. *Zostera asiatica* Miki

Zostera subgenus **Zosterella** (Ascherson) Ostenfeld

5. *Zostera noltii* Hornemann
6. *Zostera japonica* Ascherson et Graebner
7. *Zostera capensis* Setchell
8. *Zostera capricorni* Ascherson
9. *Zostera muelleri* Irmisch ex Ascherson
10. *Zostera mucronata* den Hartog
11. *Zostera novazelandica* Setchell

Phyllospadix W.J. Hooker

12. *Phyllospadix scouleri* W.J. Hooker
13. *Phyllospadix torreyi* S. Watson
14. *Phyllospadix serrulatus* Ruprecht ex Ascherson
15. *Phyllospadix iwatensis* Makino
16. *Phyllospadix japonicus* Makino

? *Phyllospadix juzepczukii* Tsvelev (see footnote*)

Heterozostera (Setchell) den Hartog

17. *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog
18. *Heterozostera polychlamis* Kuo
19. *Heterozostera nigricaulis* Kuo
20. *Heterozostera chilensis* Kuo

Cymodoceaceae

Halodule Endlicher

21. *Halodule uninervis* (Forsskål) Ascherson
22. *Halodule beaudettei* (den Hartog) den Hartog
23. *Halodule wrightii* Ascherson
24. *Halodule bermudensis* den Hartog
25. *Halodule ciliata* den Hartog
26. *Halodule pinifolia* (Miki) den Hartog
27. *Halodule emarginata* den Hartog

Cymodocea König in König et Sims

28. *Cymodocea nodosa* (Ucria) Ascherson
29. *Cymodocea rotundata* Ehrenberg et Hemprich ex Ascherson
30. *Cymodocea serrulata* (R. Brown) Ascherson et Magnus
31. *Cymodocea angustata* Ostenfeld

Syringodium Kützing in Hohenacker

32. *Syringodium filiforme* Kützing in Hohenacker
33. *Syringodium isoetifolium* (Ascherson) Dandy

Thalassodendron den Hartog

34. *Thalassodendron ciliatum* (Forsskål) den Hartog
35. *Thalassodendron pachyrhizum* den Hartog

Amphibolis C. Agardh

36. *Amphibolis antarctica* (Labillardière) Sonder et Ascherson
37. *Amphibolis griffithii* (J.M. Black) den Hartog

Posidoniaceae

Posidonia König in König et Sims
38. *Posidonia oceanica* (Linnaeus) Delile
39. *Posidonia australis* J.D. Hooker
40. *Posidonia sinuosa* Cambridge et Kuo
41. *Posidonia angustifolia* Cambridge et Kuo
42. *Posidonia ostenfeldii* den Hartog
43. *Posidonia robertsoniae* Kuo et Cambridge
44. *Posidonia coriacea* Cambridge et Kuo
45. *Posidonia denhartogii* Kuo et Cambridge
46. *Posidonia kirkmanii* Kuo et Cambridge

Hydrocharitaceae

Vallisnerioideae

Enhalus L.C. Richard
47. *Enhalus acoroides* (Linnaeus *f*.) Royle

Thalassioideae

Thalassia Banks ex König in König et Sims
48. *Thalassia hemprichii* (Ehrenberg) Ascherson in Petermann
49. *Thalassia testudinum* Banks ex König in König et Sims

Halophiloideae

Halophila Du Petit Thouars

Halophila sect. **Halophila**
50. *Halophila ovalis* (R. Brown) J.D. Hooker
    ssp. *ovalis*
    ssp. *bullosa* (Setchell) den Hartog
    ssp. *linearis* (Den Hartog) den Hartog
    ssp. *ramamurthiana* Ravikumar et Ganesan
51. *Halophila ovata* Gaudichaud in Freycinet
52. *Halophila minor* (Zollinger) den Hartog
53. *Halophila australis* Doty et Stone
54. *Halophila hawaiiana* Doty et Stone
55. *Halophila madagascariensis* Steudel ex Doty et Stone
56. *Halophila johnsonii* Eiseman in Eiseman et McMillan
57. *Halophila stipulacea* (Forsskål) Ascherson
58. *Halophila decipiens* Ostenfeld
59. *Halophila capricorni* Larkum

Halophila sect. **Microhalophila** Ascherson
60. *Halophila beccarii* Ascherson

Halophila sect. **Spinulosae** Ostenfeld
61. *Halophila spinulosa* (R. Brown) Ascherson

Halophila sect. **Tricostatae** Greenway
62. *Halophila tricostata* Greenway

Halophila sect. **Americanae** Ostenfeld
63. *Halophila engelmanni* Ascherson
64. *Halophila baillonii* Ascherson ex Dickie in J.D. Hooker

Ruppiaceae

Ruppia Linnaeus
65. *Ruppia* aff. *tuberosa* (den Hartog, in prep., not yet formally described)

Zannichelliaceae

Lepilaena Drummond ex Harvey
66. *Lepilaena marina* E.L. Robertson in Womersley

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*See the discussion under "**Phyllospadix** Hooker". The authors of this chapter have not had the opportunity to study material of this species. Its description, however, is insufficiently clear to distinguish it from other species of *Phyllospadix*. For this reason we have not given it a number in the list.

Chapter 2

Seagrass Evolution, Ecology and Conservation: A Genetic Perspective

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I. Introduction

The study and characterization of natural systems involves the evaluation of their diversity and the identification and definition of processes and fluxes operating at different temporal and spatial scales. Ecological studies in general are limited by their ability to infer these different scales of process. The use of genetic analysis to provide insight into scales of process in ecology has increased as the basic tools to undertake such studies have improved and become more widely available. A large number of genetic based approaches are available today but most commonly utilized are DNA markers to assess the relationships among individuals at hierarchical levels ranging from fine scale population processes to the phylogenetic relationships of species, genera, and higher taxa. To date, most studies of seagrass genetic diversity have been aimed toward the comprehension of ecological and evolutionary processes and, as such, this is the main subject of this chapter. However, we also provide insight into how seagrass genetic diversity can be assessed and utilized for biodiversity conservation, although the use of this approach has been very limited to date (Waycott, 2000a). As genetic diversity data provide insight into such an array of evolutionary and ecological processes it represents valuable information for conservation management strategies (e.g. Ehrlich and Wilson, 1991; Faith, 1994; Moritz and Faith, 1998). The widespread use of genetic data in conservation (e.g. Frankel and Soule, 1981; Frankel et al., 1995; Holsinger et al., 1999; Frankham et al., 2002) has allowed dramatic improvement in our ability to interpret patterns of genetic diversity in this context.

Seagrasses represent difficult ecological subjects in marine ecosystems. The biology of seagrasses is constrained by the environment they inhabit leading to convergence in morphologies. For example the majority of seagrass species possess flexible strap-like leaves (den Hartog, 1970), although they do not represent a single evolutionary lineage (Les et al., 1997). This leaf form allows the plants to thrive in their fluidic, tide- and wave-driven

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environment. The evolutionary trends that have lead to these, and other convergent characteristics, are difficult to interpret without adequate insight into their origins in both an ecological and evolutionary context. Significantly, the suite of seagrass adaptations (see "Foreword") represents dramatic evidence of the adaptive capacity of flowering plants to evolve and survive in extreme environments and as such warrants careful study.

Our understanding of seagrass ecology, physiology and adaptation has been constrained by our ability to develop a clear understanding of many biological features of these plants such as their ability to pollinate in water (Cox, 1993; Ackerman, 1995; Verduin, 1996; Ackerman, Chapter 4). In contrast the details of seagrass photosynthetic mechanisms (as inferred through the application of PAM, e.g. Larkum et al., Chapter 14) during different phases of their daily, weekly or monthly growth are rapidly being unravelled due to the now widespread use of new technologies. However, some of the most basic questions of biology such as evolutionary relatedness, plant (genet) age and growth, selection for adaptive traits, breeding system, and disturbance response strategies, are poorly studied. It is now possible to investigate these questions using a range of readily available DNA based markers (for review see Reusch, 2001b). With these techniques we can now study almost any level in the hierarchy of seagrass relationships and population processes (Les et al., 1997; Waycott, 2000a; Waycott, 2000b; Reusch, 2001b).

The use of genetic markers to study questions of seagrass evolution and ecology began during the 1980–1990s (Les, 1988; McMillan, 1991; Triest, 1991a). These earlier studies largely concluded that seagrasses were remarkable in their genetic uniformity indicating that the application of allozyme data to the study of population processes would not be fruitful. However, later studies (Laushman, 1993; Ruckelshaus, 1995; Waycott, 1995; Williams and Davis, 1996; Waycott et al., 1997), demonstrated that greater sampling efforts could better detect genetic polymorphism thus improving the utility of allozyme markers. The introduction of readily applied DNA markers provided significantly greater sensitivity (Alberte et al., 1994; Procaccini et al., 1996; Reusch et al., 1999c).

In this chapter, we discuss the outcomes of genetic approaches to the study of seagrass biology. Our aim is to provide insight into the outcomes gained from the use of powerful molecular based methodologies. We do not attempt to explain these methods, as many other reviews are available (e.g. Bachmann, 1994; Jarne and Lagoda, 1996; Mueller and Wolfenbarger, 1999; Ouborg et al., 1999; Bachmann, 2001; Reusch, 2001b; Gibson, 2002; Judd et al., 2002) and we direct the reader to these sources for further details and additional literature. This chapter includes two major sections. The first discusses molecular systematics and insights obtained from its application, as an approach independent of earlier exclusively morphological based methods. This section deals first with the systematic placement of families and insights gained from recent large-scale molecular phylogenetic analyses of the entire monocotyledon subclass (Alismatidae) that contains the seagrasses. We then discuss the current state of molecular based intrageneric studies and the insights they provide into seagrass evolution. The second section is concerned with genetic approaches to the investigation of ecological and population processes including seagrass growth, reproduction and adaptation.

II. The Evolution of Seagrass Diversity

A. Classification and Higher Level Relationships

Early impressions of seagrass relationships reflected superficial morphological comparisons to other plant groups. These crude concepts are illustrated by the 1792 generic name *Phucagrostis* Cavolini (literally 'seaweed grass'), now a synonym of *Cymodocea* K. D. Koenig. Agardh (1821) actually included *Amphibolis antarctica* among the algae (Sauvageau, 1891) and the marine angiosperms remained less studied than most algae throughout the mid 19th Century (Ascherson, 1867). Eventually, their angiospermous affinity was elucidated, but misconceptions regarding their precise relationships persisted. Delpino (1870) regarded *Zostera* as an aquatic aroid (Araceae) and *Posidonia* as an aquatic grass (Poaceae) (Schenck, 1886/2003). However, by the early 20th Century, authors consistently accepted the placement of all seagrasses within the monocotyledonous Helobiae (subclass Alismatidae).

Endlicher (1836–1840) included *Thalassia* among the genera of 'Fluviales' such as *Althenia*, *Cymodocea*, *Halodule*, *Posidonia*, *Ruppia*, and *Zostera*. However, other authors placed *Enhalus*,

Table 1. Comparison of selected marine angiosperm (seagrass) classifications.

Marine genera	Ascherson and Graebner (1907)	Arber (1920)	Sculthorpe (1967)	Den Hartog (1970)	Cronquist (1981)	Tomlinson (1982)	Dahlgren et al. (1985)	Thorne (1992)	Les et al. (1997)
Enhalus	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD
Halophila	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD
Thalassia	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD	HYD
Amphibolis	POT	POT	ZAN	POT	CYM	CYM	CYM	CYM	CYM
Cymodocea	POT	POT	ZAN	POT	CYM	CYM	CYM	CYM	CYM
Halodule	POT	POT	ZAN	POT	CYM	CYM	CYM	CYM	CYM
Heterozostera	–	–	ZOS	POT	ZOS	ZOS	ZOS	ZOS	ZOS
Lepilaena[a]	POT	–	ZAN	–	ZAN	ZAN	ZAN	ZAN	ZAN
Phyllospadix	POT	POT	ZOS	POT	ZOS	ZOS	ZOS	ZOS	ZOS
Posidonia	POT	POT	POS	POT	POS	POS	POS	POS	POS
Ruppia	POT	POT	RUP	POT	RUP	POT	POT	POT	RUP
Syringodium	POT	–	ZAN	POT	CYM	CYM	CYM	CYM	CYM
Thalassodendron	POT	–	–	POT	CYM	CYM	CYM	CYM	CYM
Zostera	POT	POT	ZOS	POT	ZOS	ZOS	ZOS	ZOS	ZOS

[a] Not identified as marine, but included in Zannichelliaceae by Les et al. (1997).

CYM = Cymodoceaceae; HYD = Hydrocharitaceae; POS = Posidoniaceae; POT = Potamogetonaceae; RUP = Ruppiaceae; ZAN = Zannichelliaceae; ZOS = Zosteraceae. — = not considered by author.

Thalassia and *Halophila* within Hydrocharitaceae (Richard, 1811; Rohrbach, 1871; Balfour, 1879). Bentham and Hooker (1883) and Ascherson and Graebner (1907) maintained the division of seagrass species into separate families (Hydrocharitaceae, Potamogetonaceae). This arrangement was later adopted by Arber (1920), and the distinction of seagrass species in the Hydrocharitaceae has been followed since. Yet, even though seagrasses were divided among separate families, they were believed by some to retain a relatively close relationship. Balfour (1879) considered *Halophila* as the link between the families Potamogetonaceae and Hydrocharitaceae, Arber (1920) and Setchell (1920) regarded these same families as 'nearly related'.

With the exception of den Hartog (1970), who simply adopted Ascherson and Graebner's (1907) two family system, classifications increasingly partitioned seagrass genera among several additional families by the later part of the 20th Century (Table 1). den Hartog (1970) did, however, remark that Ascherson and Graebner's concept of Potamogetonaceae was heterogeneous and needed to be subdivided. Major similarities and differences in the historical family groupings of seagrass genera are shown by the selected classifications in Table 1. It is noteworthy that greater taxonomic consistency underlies these examples, because Ascherson and Graebner's dual family system (followed by Arber and den Hartog) subdivided Potamogetonaceae into tribes corresponding to Cymodoceaceae (Cymodoceeae), Posidoniaceae (Posidonieae), Potamogetonaceae (Potamogetoneae), Zannichelliaceae (Zannichellieae) and Zosteraceae (Zostereae), thus yielding the same six taxa recognized by many of the later classifications. These examples illustrate that a relatively stable seagrass classification has existed for more than a century.

However, the nature of scientific evidence in support of the assorted marine angiosperm classifications shown in Table 1 is quite variable. The earliest classifications essentially represented opinions of natural groups based on an author's perception of which taxa were most similar morphologically and anatomically. The incorporation of evolutionary theory in the 20th Century inspired the adoption of classifications that also strived to be meaningful phylogenetically with most modern classifications now being implicitly phylogenetic (Judd et al., 2002).

In early phylogenetically based studies, relationships were ascertained by identifying groups that shared a number of distinctive features, arguably indicating their common ancestry. Bessey (1915) incorporated the concept of character state polarity to help differentiate groups as relatively primitive or advanced. Otherwise, this approach did not differ materially from that used to establish putatively 'natural' classifications other than assuming that similarity resulted from a common evolutionary ancestry. Efforts to better quantify group similarity led to the incorporation of 'phenetic' approaches, which performed cluster analyses of character matrices using computerized algorithms. Such an approach was taken by Clifford (1970) who demonstrated that Cymodoceaceae, Posidoniaceae, Ruppiaceae, Zannichelliaceae and Zosteraceae were quite similar as a group, but differed considerably from Hydrocharitaceae.

The comprehensive and highly influential work by Cronquist (1981) allegedly was based on an integration of all data available at that time. That work depicted phylogenetic relationships within subclasses and among orders using tree-like diagrams; however, these were not produced using an explicit method. Similar approaches were taken by authors of other synthetic works (e.g. Dahlgren, 1980; Takhtajan, 1980). Comparable methods were used to develop quite detailed classifications of seagrasses (e.g. Tomlinson, 1982).

The incorporation of cladistic methodology led to an important refinement in phylogenetic classification, that is it established an objective methodology for reconstructing phylogenetic hypotheses. Unlike previous approaches, cladistic analyses could provide explicit details regarding the character states that defined particular relationships, which could then be depicted as a hierarchical, tree-like diagram.

The first detailed cladistic analysis of seagrass relationships was conducted by Dahlgren et al. (Dahlgren and Rasmussen, 1983; Dahlgren, 1985) as a part of their study of monocotyledons. Within the subclass Alismatidae (which contains all seagrasses), they compared the distribution of states for 56 morphological characters and provided the first explicit evolutionary framework on which to base a phylogenetic seagrass classification (Fig. 1). Their results depicted seagrasses within three distinct clades: (1) Cymodoceaceae/Zannichelliaceae, (2) Posidoniaceae/Zosteraceae and (3) Hydrocharitaceae (Ruppiaceae were merged with Potamogetonaceae). Within Hydrocharitaceae, *Enhalus* was allied with *Vallisneria* (subfamily Vallisnerioideae), whereas *Halophila* and *Thalassia* were each placed in separate subfamilies (Halophiloideae, Thalassioideae). Dahlgren (1985) also argued against the inclusion of Cymodoceaceae (incl. *Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium*, *Thalassodendron*) within Zannichelliaceae (*Althenia*, *Lepilaena*, *Zannichellia*). Cox and Humphries (1993) conducted a morphological cladistic analysis of some seagrasses, which indicated the common origin of Posidoniaceae, Cymodoceaceae, and Zosteraceae. However, their analysis excluded many non-seagrass families necessary to evaluate this question adequately, thereby yielding unfounded results (see Les et al., 1997). Les and Haynes (1995) reanalysed the Alismatidae data of Dahlgren (1985) using a computer program capable of recovering additional maximum parsimony reconstructions and also performed new analyses using corrected data. Although the results were similar to Dahlgren's original study, a number of discrepancies indicated that morphological data alone could not be relied on to provide compelling support for relationships in this group.

Incorporation of molecular data in cladistic analyses provided the next major refinement in phylogenetic reconstructions of seagrass relationships. Les et al. (1993) conducted preliminary cladistic analyses of Alismatidae using *rbcL* gene sequence data from 8 families, but included only a few seagrass genera, which did not provide much insight into their relationships. In an *rbcL* analysis expanded to include 25 genera from all 15 alismatid families, Les and Haynes (1995) began to disclose consistent seagrass clades representing (1) Hydrocharitaceae, (2) Posidoniaceae/Ruppiaceae/Cymodoceaceae, (3) Zosteraceae, and (4) Zannichelliaceae (*Lepilaena*). Seagrass relationships were evaluated further in more comprehensive *rbcL* analyses of 55–69 alismatid species (eventually including 23 seagrass species from all 14 marine genera) which specifically addressed the question of the number of seagrass origins (Waycott and Les, 1996; Les et al., 1997) (Fig. 1).

The *rbcL* survey by Les et al. (1997) indicated that marine angiosperms have evolved in at least three separate lineages. Another independent lineage (Zannichelliaceae), which contains *Lepilaena marina*, represents a fourth marine angiosperm origin given that this species (with several others in the genus) is known to occupy marine habitats (Womersley, 1984). To date, the study by Les et al. (1997) remains the most complete molecular phylogenetic analysis of seagrass interrelationships at the genus and family level. Procaccini et al. (1999b) used *trnL* intron sequence data to study relationships among six marine genera in five families and recovered distinct clades containing (1) *Cymodocea*/*Posidonia*/*Ruppia*, (2) *Zostera*/*Phyllospadix* and (3) *Halophila*, thus in agreement with the *rbcL* analysis by Les et al. (1997).

Molecular phylogenetic analyses have begun to clarify some finer details of seagrass relationships. First, the emerging pattern of phylogenetic relationships indicates that seagrasses should be divided

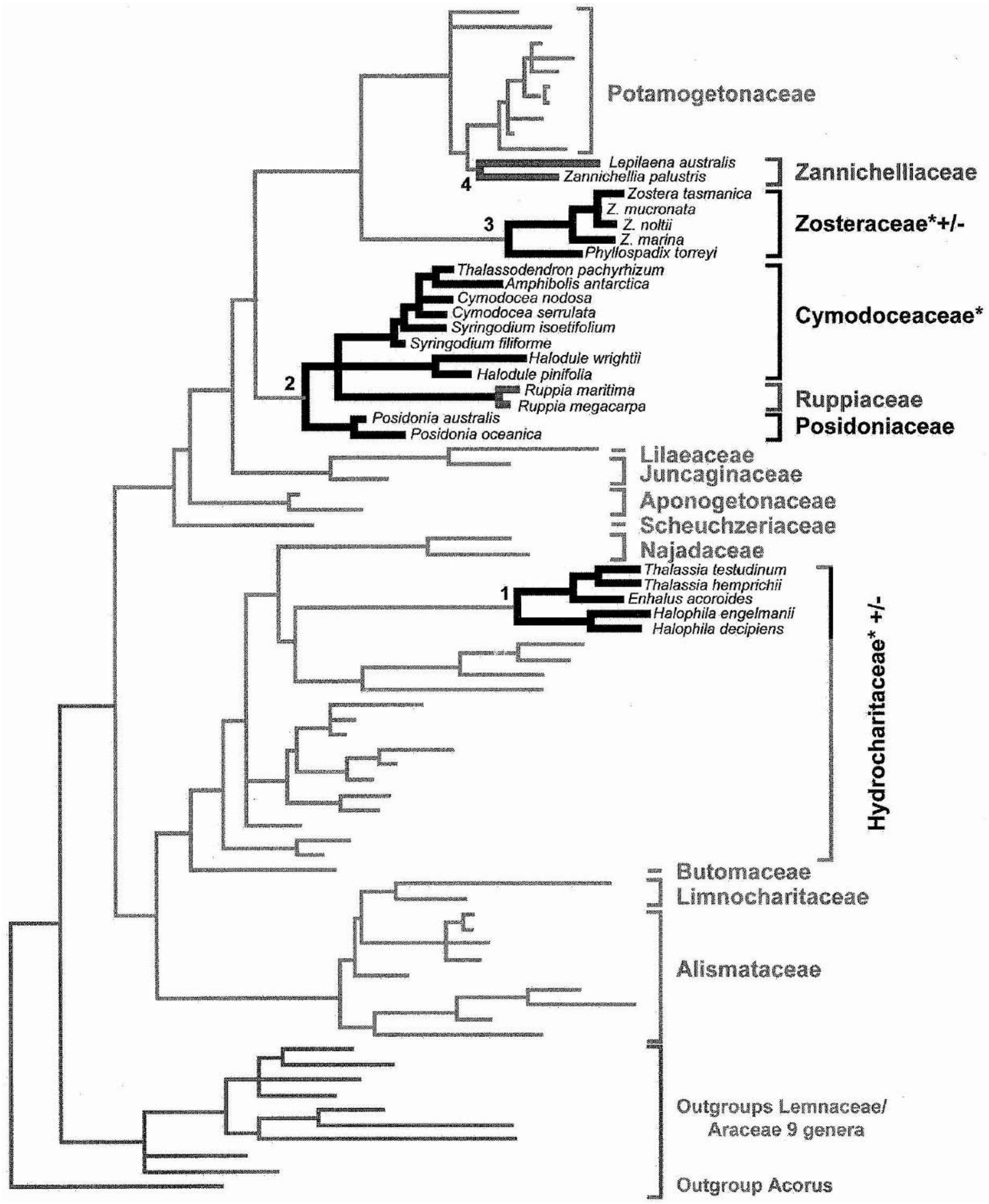


Fig. 1. Alismatid phylogeny based on *rbcL* cpDNA sequence data (adapted from Les et al., 1997). Family designations are shown defined in Les et al. (1997) and seagrass species are listed, for full details see Les et al. (1997). Seagrass taxa exhibiting a dioecious breeding system are indicated (*).

among six separate families (Table 1, last column) in preference over classification systems that recognize fewer families. Moreover, it is now evident that Ruppiaceae are closely allied with Posidoniaceae and Cymodoceaceae rather than representing a subdivision of the freshwater family Potamogetonaceae. Molecular analyses also confirm the distinctness of the Zosteraceae and remote relationship of marine Hydrocharitaceae to all other seagrasses. Finally, molecular studies have provided compelling evidence that marine Hydrocharitaceae occur within a single, monophyletic clade, thereby invalidating classifications of the family that divide the three marine genera otherwise among the freshwater representatives.

At this time, higher-level seagrass relationships appear to be clarified quite adequately, at least well enough to provide a meaningful, defensible classification. Additional sequence data could corroborate the integrity of seagrass clades further, but would unlikely result in any major alterations of phylogenetic relationships already disclosed at higher levels. Instead, more emphasis should be made to continue refining phylogenetic relationships at lower, i.e. interspecific levels within seagrass genera (see below).

B. Interspecific Relationships

Cladistic analyses of molecular and non-molecular data have been applied to questions of seagrass species relationships, but this approach only has been taken relatively recently and many species remain unstudied. Overall, seagrasses are not diverse with most genera being quite species poor.

Enhalus (Hydrocharitaceae) is regarded as monotypic, comprising the sole species *E. acoroides.* Araño et al. (2003) reported a complete lack of detectable RFLP variation among *E. acoroides* populations from different geographical regions, which would support the existence of a single *Enhalus* species. However, a recent comparison of ITS sequences from Chinese and Australian material of *Enhalus* show that they are quite distinct (Les and Moody, unpublished). Further investigation of *Enhalus* is warranted and may disclose the existence of additional species.

Four marine genera (*Amphibolis*, *Syringodium*, *Thalassia*, *Thalassodendron*) each contain only two species, thus showing unequivocal intrageneric phylogenetic relationships if the genera are truly monophyletic. Les et al. (1997) included both species of *Syringodium* and *Thalassia*, which confirmed the monophyly of *Thalassia*, but not *Syringodium* (paraphyletic with *Cymodocea*). The monophyly of *Thalassia* and its subdivision into two species (Old and New Worlds) has been demonstrated further by molecular sequence data from nuclear (18S, ITS) and other cpDNA (*trnL*) loci. The monophyly of *Amphibolis* and *Thalassodendron* (sister genera in *rbcL* analyses) could be tested similarly by obtaining *rbcL* sequences for *Amphibolis griffithii* and *Thalassodendron ciliatum* to include within the data in Les et al. (1997). Only two of the four *Cymodocea* species were included in the *rbcL* analysis and it would be desirable to obtain data for the unsampled species (*C. rotundata*, *C. angustata*) as well. Further details of relationships in the *Amphibolis*/*Cymodocea*/*Syringodium*/*Thalassodendron* clade should be investigated by sampling all 10 species using *rbcL* and additional molecular loci as well as incorporating a complete morphological data set. Precise delimitation of generic boundaries in this group of seagrasses remains unsettled.

Halodule (three species, plus) has been well investigated using nuclear (ITS) and cpDNA (*rbcL*, *trnL*) markers (Les et al., 1997; Waycott, unpublished), yet relationships remain complicated. All markers (ITS, *rbcL*, *trnL*) examined thus far show the genus to be monophyletic. Within the genus, nuclear (ITS) sequence data analysis yielded one monophyletic clade comprising the New World *H. wrightii* and another containing the Old World *H. pinifolia* and *H. uninervis* (Fig. 2A). Populations of the latter two species overlap and are not clearly differentiated by ITS data. However, cpDNA (*trnL*) data show considerable overlap among populations of all three species, thus complicating the interpretation of the molecular analyses (Fig. 2B). *Halodule* would benefit from a genus wide intensive study of population level relationships.

Posidonia (five species) has been studied cladistically using morphological data and molecular sequence data from nuclear (ITS) and cpDNA (*rbcL*; *trnL*) loci. Phylogenetic analyses of these different data sets are consistent and indicate a similar overall pattern of relationships in the genus. Combination of these congruent data sets (Waycott and Les, unpublished data) suggests that the Mediterranean *P. oceanica* (the outlier geographically) is basal, with the Australian taxa derived (Fig. 3). *Posidonia sinuosa*, *P. australis* and *P. angustifolia* are relatively

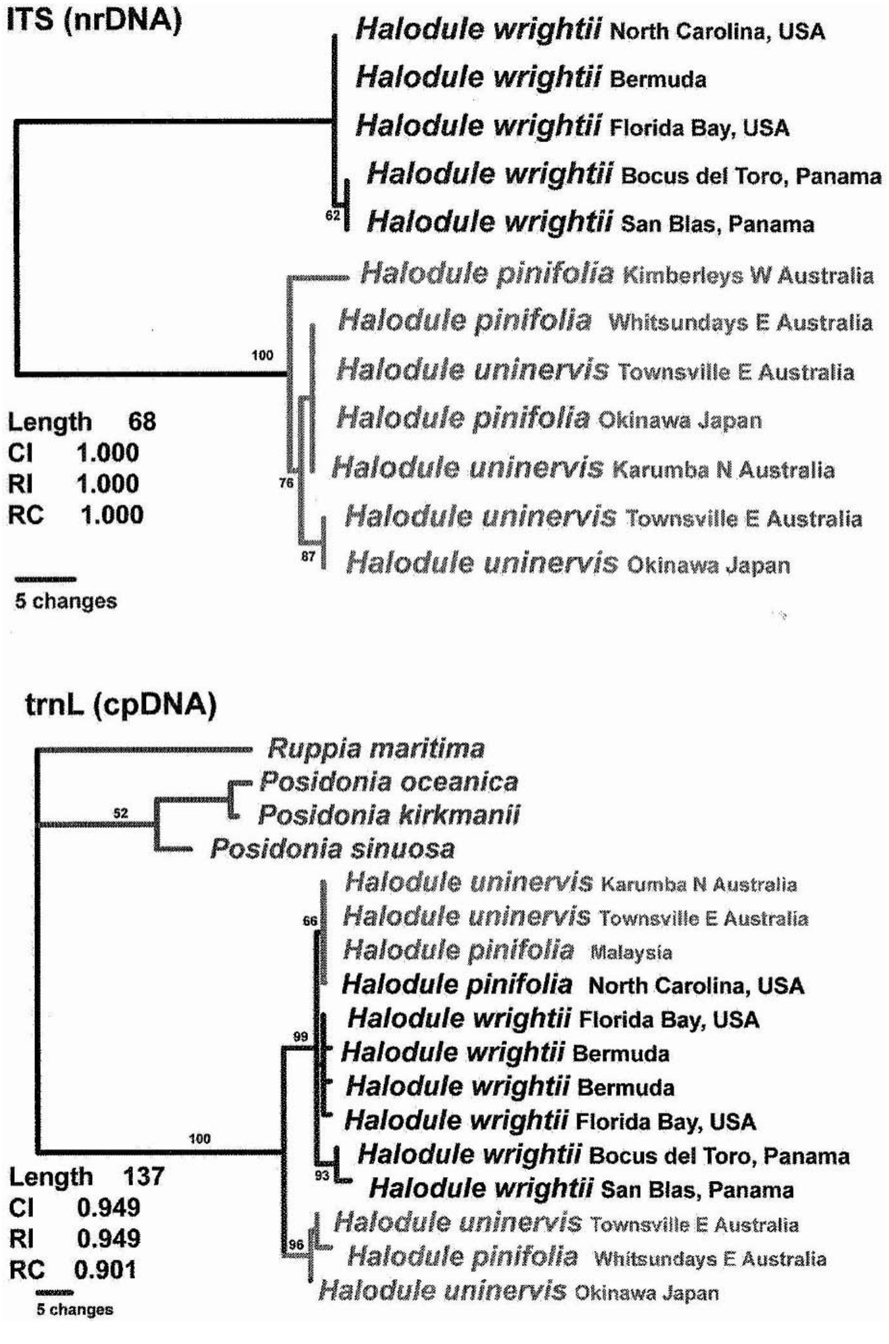


Fig. 2. (a) Above ITS and (b) below *trn*L parsimony phylogram of the genus *Halodule* (bootstrap support shown adjacent to nodes), localities of collections shown next to species name (Waycott and Barnes unpublished).

distinct (the latter two representing closely related sister species); however, the five remaining Australian taxa (*P. coriacea*, *P. ostenfeldii*, *P. robertsonii*, *P. denhartogii*, *P. kirkmanii*) appear to represent only minor variants of a single species and are indistinct both morphologically and genetically.

A phylogenetic study of *Halophila* has been conducted by Waycott et al. (2002) who analysed ITS data from 36 accessions of 11 recognized species.

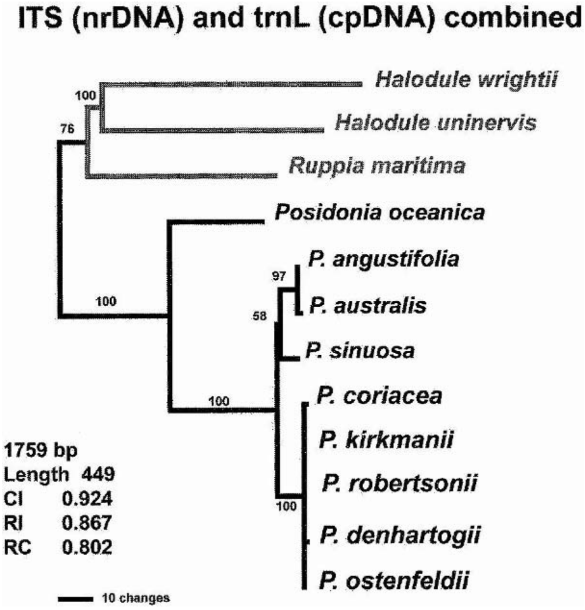


Fig. 3. Combined data of ITS and *trn*L parsimony phylogram of *Posidonia* (bootstrap support shown adjacent to nodes), localities of collections shown next to species name (Waycott and Les unpublished).

Their results dispute the taxonomic limits of *H. ovalis*, wherein some populations are closely related to *H. australis*. The rare *H. johnsonii* and *H. hawaiiana* were not separable from *H. ovalis* by ITS data and perhaps represent only minor variants of a single species. However, most other species appear to be distinct and are associated with a pattern of vegetative reduction proceeding phylogenetically from complex leaf arrangements to reduced, simplified phyllotaxy (Fig. 4). Two *Halophila* species (*H. capricorni*, *H. baillonis*) remain unsurveyed for ITS. It has also been observed that rDNA can accumulate pseudogenes, making the verification of sequences important before use in analyses of relationships (Ruggiero and Procaccini, 2004). Additional loci (especially cpDNA) should be surveyed to seek further support for relationships disclosed by the initial ITS data analysis.

Systematic relationships within *Phyllospadix* (five species) have not been investigated in any detail. Isozyme patterns have been compared for three species, with higher similarity reported between *P. scouleri* and *P. torreyi* than between either species or *P. serrulatus* (Triest, 1991b). *Phyllospadix* would benefit from a thorough evaluation of taxonomic limits and relationships using both molecular and morphological data sets.

Relationships within *Zostera* (nine species including *Heterozostera*) have now been studied in some detail. Chromosome morphology is distinct between subgenera with those of subgenus *Zostera* smaller than those of subgenus *Zosterella* (Uchiyama, 1996). Similarly, isozymes show different patterns between *Z. marina* (subg. *Zostera*) and species of subgenus *Zosterella*; however, only slight isozymic differences were observed among *Z. capensis*, *Z. capricorni*, *Z. muelleri,* and *Z. novazelandica* (subgenus *Zosterella*) (Triest, 1991b). Uchiyama (1996) conducted a molecular analysis of three *Zostera* species using 18s RDNA RFLP data. His results also showed differences between species of different subgenera, but sampling was insufficient to address relationships in detail. Les et al. (1997) surveyed three *Zostera* species (representing both subgenera) in their *rbcL* analysis of Alismatidae. Again, species from the different subgenera were considerably divergent. Les et al. (1997) also provided evidence that the taxon formerly recognized as a separate genus (*Heterozostera tasmanica*) falls within the genus *Zostera* phylogenetically and should be included within *Zostera*. (Les et al., 2002) performed a morphological phylogenetic analysis of all *Zostera* species (including *Heterozostera*) and also evaluated systematic relationships among eight taxa using a combined data set consisting of DNA sequences from ITS, *rbcL*, and the *trnK* intron. Results of this study reinforced earlier work that indicated significant morphological and molecular divergence between the two subgenera of *Zostera* (Fig. 5). However, there was no phylogenetically defensible structure to accessions sampled for *Z. capensis*, *Z. capricorni*, *Z. muelleri,* and *Z. novazelandica*, leading to the recognition of only one variable species (*Z. muelleri*) in that group. This study verified that *Heterozostera* should be merged with *Zostera*. Recently, Les and Moody (unpublished) obtained ITS sequences from an extremely broad-leaved accession of *Zostera* from California (USA), which has been referred to as *Zostera latifolia* by some authors. Setchell (1927) regarded *Z. latifolia* to be an ecological variant of *Z. marina*. Les and Moody detected only a single substitution in the entire ITS region between the broad-leaved form from California and narrow-leaved material of *Zostera marina* from the east coast (Connecticut, USA), evidence that supports Setchell's merger of these taxa, despite conspicuous morphological difference in leaf size. These results are supported by the work of Tanaka

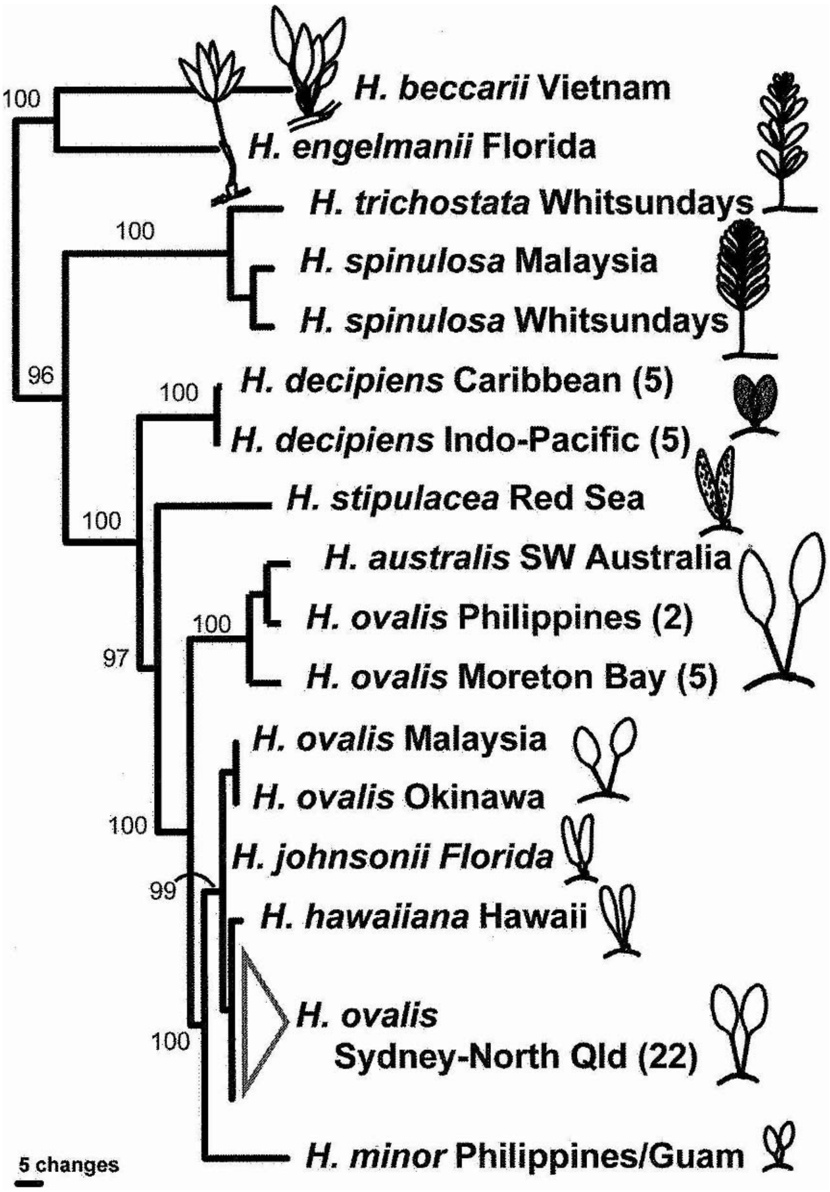


Fig. 4. ITS parsimony phylogram of *Halophila* (bootstrap support shown adjacent to nodes), localities of collections shown next to species name (adapted from Waycott et al., 2003).

et al. (2003) who analysed the chloroplast gene region *matK*. Their results suggest that *Z. noltii* and *Z. japonica* are sister to the combined taxon *Z. muelleri* (=*Z. capricorni* of Les et al., 2002). Further exploration of the intrageneric relationships would be useful to provide insight into suggestions of creating additional genera within the family by Tomlinson and Posluszny (2001).

The taxonomy and systematics of *Ruppia* is in serious need of study. Until recently, *Ruppia* had been placed within the family Potamogetonaceae, usually as a separate subfamily. Les et al. (1993) showed that *rbcL* data placed *Ruppia* closer to Cymodoceaceae (*Syringodium*). The alliance of Cymodoceaceae, Ruppiaceae, and Posidoniaceae was verified in later, more comprehensive studies (Waycott and Les, 1996; Les et al., 1997). The actual number of *Ruppia* species is not known with any certainty. Cook (1996) reported 2–10 species worldwide. The study by Les et al. (1997) included only

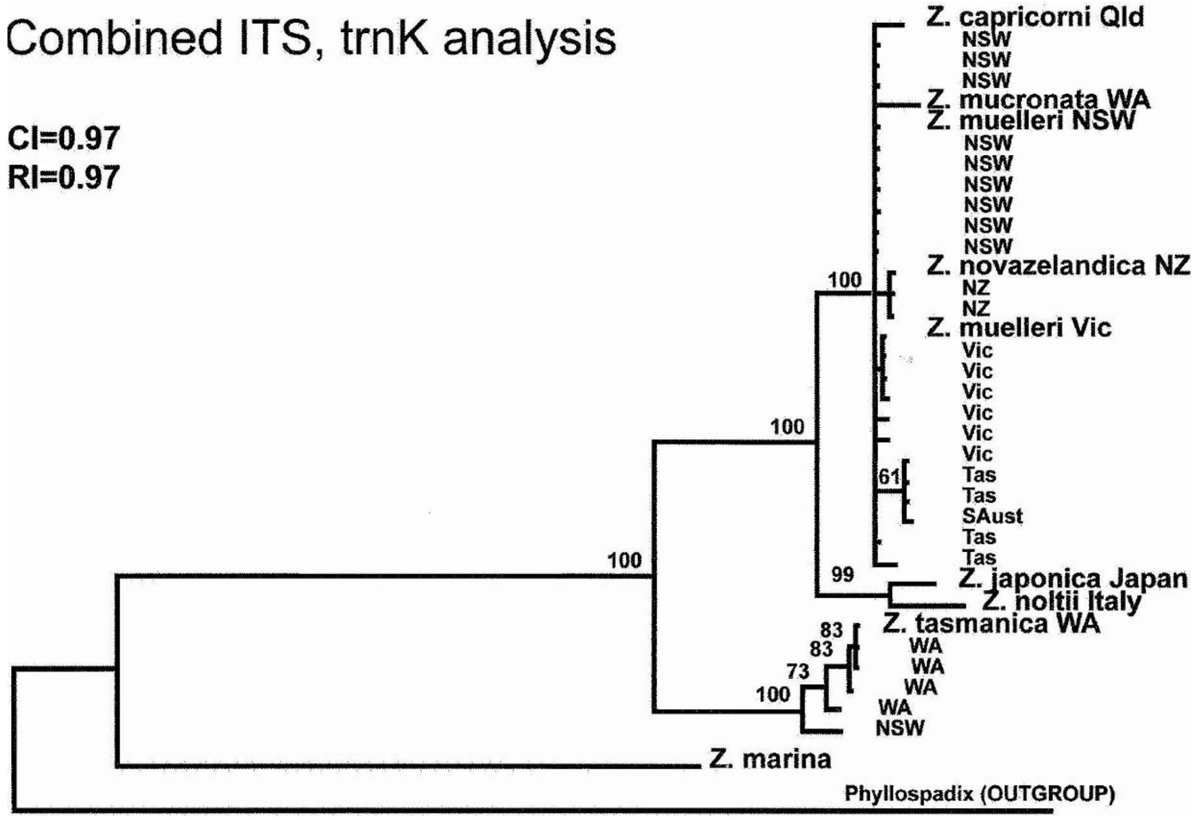


Fig. 5. Combined data of ITS and *trn*L parsimony phylogram of *Zostera* (bootstrap support shown adjacent to nodes), localities of collections shown next to species name (adapted from Les et al., 2002).

two species (*R. maritima* from North America, *R. megacarpa* from Australia) whose *rbcL* sequences were fairly distinct. Guha and Mondal (1999) studied pollen morphology in *Ruppia* and concluded a worldwide revision of *Ruppia* which includes a full appraisal of morphological characters as well as molecular phylogenetic analyses will be necessary before further systematic details such as species boundaries and relationships can be ascertained in this genus.

Lepilaena (five species; Zannichelliaceae) also has not been studied systematically in any great detail. Molecular (*rbcL*) data clearly showed *Lepilaena australis* as related to *Zannichellia*, but other species await study. Two species (*Lepilaena marina*; *L. cylindrocarpa*) are truly marine (Womersley, 1984) and it would be informative to determine whether the marine habit is basal or derived in this genus of otherwise freshwater species. Although quite likely, the monophyly of *Lepilaena* has not yet been verified by phylogenetic analysis.

These studies have all verified the utility of detailed analysis of the intraspecific variation across a wide geographic range for seagrass species using DNA sequence data and careful phylogenetic analysis. Broader scale studies may require considerable effort in obtaining samples from extremes of the range of species to better describe the finer scale evolutionary trends within genera and species. These types of study begin to impinge upon the traditional population genetic approach to understanding relatedness of seagrass populations as will be discussed in the following sections. The intersection of these two fields of study represents the investigation of species phylogeography (e.g. for review see Avise, 2000). This field of research has barely been touched in seagrasses and while at present markers that adequately detect the historical biogeographic processes are unavailable (Schaal et al., 1998), future research will proved invaluable to the study of broad scale evolution of seagrass species. The field of molecular systematics is undergoing continuous and rapid development and this will provide fertile ground for future research activities.

III. Ecological and Reproductive Processes

A. Species-Wide Population Genetic Studies

1. Introduction

Seagrasses are distributed in coastal areas of all continents and belong to nine species assemblages (floras), six of which are exclusively temperate (Duarte, 2001). Distributional ranges of single species can differ radically; ranging from species whose distribution is limited to a single flora (e.g. *Posidonia oceanica* in the Mediterranean) to widely distributed species such as *Zostera marina*. The present distribution of seagrass species is the result of processes occurring at a number of different temporal scales and may reflect events that occurred a very long time ago (tens of thousands of years or more). However, the actual distribution of populations is also the result of ongoing extant dynamic processes of colonization/extinction. When population distributions are viewed using a genetic perspective, higher genetic differentiation among populations reflects lower genetic exchange (gene flow) and indicates longer-term isolation. The application of molecular markers to study levels of population connectivity potentially can provide significant insights into the factors influencing present-day distribution of seagrass species, particularly when applied across broad spatial scales.

Almost half of the roughly 65 papers published on seagrass population genetic studies attempt to quantify gene flow among distinct populations (Table 2). To date studies addressing the broad scale distribution genetic diversity has only been documented for a few species (Table 2). However, there are many studies in progress on different species with new and potentially more polymorphic molecular markers. When viewed across all the broader scale studies, levels of population connectivity are not always related to differences in dispersal mode or reproductive characteristics among species, and do not appear to be linked to their phylogenetic relatedness.

Only few species have been studied in detail: within the genus *Posidonia*, only the Australian endemic *P. australis* and the Mediterranean endemic *P. oceanica*; within the genus *Zostera*, only *Zostera marina* from Europe and North America and in the genus *Thalassia*, only the Caribbean species, *Thalassia testudinum* (these species are the subject of individual chapters in this volume, see Chapters 16, 17 and 18).

2. Posidonia australis

A broad scale study of 20 *P. australis* populations has been performed with RAPD and allozyme markers (Waycott et al., 1997; Waycott, 1998). Populations have been sampled along their geographical range, from the north-western populations of Shark Bay, in warm-subtropical waters, to the eastern populations of Lake Macquarie. RAPDs detected higher genotypic variability compared to allozymes, although in a few cases the authors observed the opposite result. In general, populations showed high variability, with average RAPD Dg values of 0.91. Nevertheless, the analyses showed the existence of low population connectivity ($G\mathrm{st} = 0.623$) at the scale surveyed and identified regions with significant differences in genetic diversity. Meadows sampled in the south-western region show highest allozyme diversity, whereas lower diversity was recorded at the extremes of the range. Interestingly, regions with higher genetic diversity corresponded to regions of highest species diversity within the genus (Kuo and Cambridge, 1984; Waycott et al., 1997). Explanations for this pattern of species diversity may reflect the selective pressures experienced by the Australian species of *Posidonia*, which reached their current distribution from refugia occupied following Gondwanan break up millions of years ago. Selective pressures may have facilitated speciation and high genetic variability within some of the species. A South–North oriented secondary expansion from few genotypes would explain the low allozyme diversity of the north-western populations. Patterns of phylogeographic relationships show a clear distinction between these localities and the southern and eastern populations. Ongoing local reproduction and recruitment could explain the existence of molecular based genetic diversity in such localities (Waycott et al., 1997; Waycott, 2000a). This study demonstrates the utility of sampling over a very wide range to infer broader processes such as the observation of low diversity in some populations and high diversity in others (Waycott, 1998).

Table 2. Seagrass population genetic studies. The aim of each study has been classified as either: W = within population genetic diversity, B = between population genetic diversity, MS = mating system analysis, T = marker development, R = restoration studies.

Study species	Methodology	Study aim	References
Amphibolis antarctica	Allozymes, DNA fing.	W, B	1
A. griffithii	Allozymes, DNA fing.	W, B	1
Cymodocea nodosa	RAPD, SSR	W, T	2–5
Halodule wrightii	RAPD	W, B	6
Halophila decipiens	RAPD	W, B	7
H. engelmannii	RAPD	W, B	7
H. hawaiiana	SSR	B	8
H. johnsonii	RAPD	W, B	7,9
H. stipulacea	RAPD, DNA seq.	W, B	10–11
Posidonia australis	Allozymes, RAPD	W, B, MS	12–15
P. coriacea	Allozymes,	W	16
P. oceanica	Allozymes, RAPD, SSR, DNA fing.	W, B, T, R, MS	17–33
Thalassia testudinum	RAPD	W, B	34–37
Thalassodendron ciliatum	RAPD	W, B	38
Zostera marina	Allozymes, DNA fing., SSR, DNA seq.	W, B, T, R, MS	39–64
Z. noltii	SSR	W, B, T	65–66

DNA fing. = multilocus DNA fingerprinting; RAPD = Randomly Amplified Polymorphic DNA; SSR = Simple Sequence Repeats (microsatellites); DNA seq. = DNA sequencing.

1. Waycott et al. (1996); 2. Alberto et al. (2001); 3. Alberto et al. (2003b); 4. Procaccini and Mazzella (1996); 5. Ruggiero et al. (in press) 6. Angel (2002); 7. Jewett-Smith et al. (1997); 8. McDermid et al. (2003); 9. Freshwater et al. (2003); 10. Procaccini et al. (1999a); 11. Ruggiero and Procaccini (2004); 12. Waycott (1995); 13. Waycott et al. (1997); 14. Waycott and Sampson (1997); 15. Waycott (1998); 16. Campey et al. (1999); 17. Alberto et al. (2003a); 18. Capiomont et al. (1996); 19. Dalmazio et al. (2002); 20. Franconi and Barcaccia (1995); 21. Jover et al. (2003); 22. Orsini et al. (2001); 23. Procaccini et al. (1996); 24. Procaccini and Mazzella (1996); 25. Procaccini and Mazzella (1998); 26. Procaccini and Waycott (1998); 27. Procaccini et al. (2000); 28. Procaccini et al. (2001); 29. Procaccini and Piazzi (2001); 30. Procaccini et al. (2002); 31. Raniello and Procaccini (2002); 32. Ruggiero et al. (2002); 33. Sandmeier et al. (1999); 34. Kirsten et al. (1998); 35. Schlueter and Guttman (1998); 36. Waycott and Barnes (2001); 37. Davis et al. (1999); 38. Bandeira and Nilsson (2001); 39. Alberte et al. (1994); 40. Billingham et al. (2003); 41. de Heij and Nienhuis (1992); 42. Fain et al. (1992); 43. Gagnon et al. (1980); 44. Hämmerli and Reusch (2002); 45. Hämmerli and Reusch (2003a); 46. Hämmerli and Reusch (2003b); 47. Hämmerli and Reusch (2003c); 48. Laushman (1993); 49. Olsen et al. (2004); 50. Reusch et al. (1999a); 51. Reusch et al. (1999b); 52. Reusch et al. (1999c); 53. Reusch et al. (1999d); 54. Reusch (2000); 55. Reusch et al. (2000); 56. Reusch (2001a); 57. Reusch (2002); 58. Reusch (2003); 59. Ruckelshaus (1995); 60. Ruckelshaus (1996); 61. Ruckelshaus (1998); 62. Williams and Davis (1996); 63. Williams and Orth (1998); 64. Williams (2001); 65. Coyer et al. (2004); 66. Coyer et al. (submitted).

For species level allozyme studies see also: McMillan (1981); (McMillan (1982) and McMillan (1991).

3. *Posidonia oceanica*

Contrasting levels of genetic diversity have also been observed within the Mediterranean basin for the congeneric species *P. oceanica*. Studies have been conducted on 33 meadows sampled along the entire distribution range of the species using microsatellite analysis. Overall genetic diversity seems to be low [average Dg = 0.727; (Procaccini et al., 2001; Procaccini et al., 2002)], with some identical genotypes present in different populations. Based on the results from published studies, *P. oceanica* appears as a genetically depauperate species as result of evolutionary processes or recent anthropogenic influence.

Populations from the western basin were genetically more polymorphic than those from the eastern Mediterranean Sea, where North Adriatic meadows were represented by only one clone (Ruggiero et al., 2002). Meadows are distinct genetically, with overall $\theta = 0.451$ (Nm $\theta = 0.304$). A clear genetic sub-division seems to exist within the basin, with the presence of three main groups representing north-western, south-western, and eastern populations (Fig. 6). The existence of defined population groups may result from processes acting on different time scales. Present surface circulation patterns of surface currents may affect gene flow and/or colonization of different areas and could account for the existence of genetic structure over the Mediterranean Sea as a whole. The genetic structure existing in the Tyrrhenian Sea, with the presence of a clear distinction between northern and southern populations (Ruggiero et al., 2002) (Fig. 6), reflects the

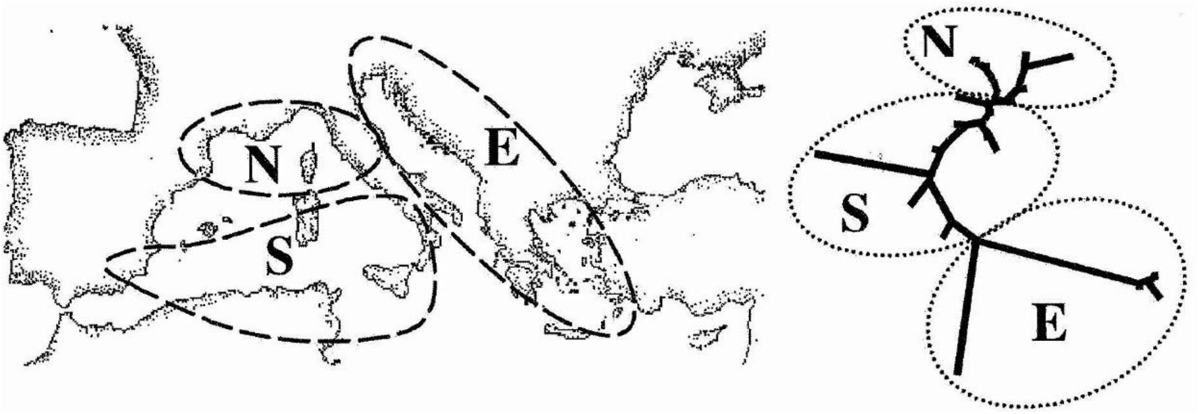


Fig. 6. Distribution of the genetic variability of *Posidonia oceanica* in the Mediterranean basin. Analysis is based on data from six microsatellite loci. Tree is based on $(\delta\mu)^2$ distance values (modified from Procaccini et al., 2002).

presence of seasonal circulation gyres in this area (Astraldi and Gasparini, 1994). The Mediterranean Sea has experienced dramatic changes of environmental parameters related to glaciations and hypersalinity crises (Maldonado, 1985; Thiede, 1978). The evolution of the basin was controlled by the interplay between geological processes and environmental parameters determining species loss and recolonisation in particular areas. Dramatic fluctuations of more than 100 m of sea water level during last glaciation surely have caused the disappearance of *Posidonia* from some areas. Thus, the actual distribution could have originated by recolonisation from populations persisting in relict zones and the low genetic variability detected in some areas could have originated from a founder effect. The latter possibility seems to be the case for the uniclonal patches of the North-Adriatic, where locally adapted genotypes are now present in the area (Ruggiero et al., 2002).

New polymorphic di-nucleotide microsatellite loci recently selected (Alberto et al., 2003a) are showing higher polymorphism levels. Preliminary analysis at basin level is confirming at broad scale the separation between eastern and western Mediterranean populations. Intra-population analyses instead are showing higher heterozygosity and clonal diversity values (Alberto et al., 2003a; Arnaud-Haond personal communication).

4. *Zostera marina*

This species has had the greatest number of publications in the genetic analysis literature for seagrasses (Moore et al., Chapter 16). Nonetheless, only recently a first study has been produced that documents the genetic diversity and genetic structure of the species throughout almost its entire geographical range (Olsen et al., 2004). This shortcoming may be due in part to the particularly widespread distribution of this species which occurs across the majority of available habitats in the northern hemisphere. Studies along the Pacific coasts of North America date back to 1992–1994 and have been carried out using RFLP (Fain et al., 1992), allozymes (Laushman, 1993) and DNA fingerprinting analyses (Alberte et al., 1994). Of these studies, DNA fingerprinting showed higher polymorphism within meadows, as expected for this marker type. More recently, other studies have utilized allozymes to compare distinct *Z. marina* meadows in California and Chesapeake Bay, showing Fst values ranging from 0.06 to 0.335, depending on the geographic distance among meadows (Williams and Davis, 1996; Williams and Orth, 1998). In the last few years, genetic diversity in *Z. marina* has been studied extensively along the northern coasts of Europe using polymorphic microsatellite loci (Reusch, 1999c among the others). The use of the same markers shows high allelic richness in the Pacific populations in respect to the Atlantic ones and clear genetic distinction between southern and northern east-Pacific populations (Olsen et al., 2004). Unfortunately, the values of polymorphism observed using microsatellites could not be compared directly with results obtained from markers utilized previously.

The aforementioned study on the distribution of microsatellite genetic diversity along the whole geographic range of the species (Olsen et al., 2004) provides a much comprehensive, comparable picture of the overall phylogeographic pattern of this species. Among the previous broader scale studies on *Zostera marina* to date, pronounced genetic sub-structuring was observed among eight European populations, with a strong linear relationship of genetic differentiation along geographic distances of 12–4,500 km (Reusch et al., 2000). However, on a larger geographic scale the observed pattern was counterintuitive, with two North American populations clustering with those from the Baltic Sea and North Sea. New data support recent genetic exchange in *Z. marina*, between the east Pacific, west and east Atlantic, suggesting a still-active trans-Arctic connections (Olsen et al., 2004). Instead, a weak correlation of genetic and geographic distance was found in populations sampled in the northern Wadden Sea and south-western Baltic Sea, indicating enhanced metapopulation dynamics in the area (Reusch, 2002). Recolonisation in the two areas may have occurred recently, masking any signal resulting from recent gene flow among populations. In general, populations showed high connectivity ($\theta = 0.018$), despite the fact that populations are annual in the Wadden Sea and perennial in the Baltic. Theoretically annual Wadden Sea populations may show higher connectivity due to greater propagule production and stronger tidal currents. The vectors of such high gene flow are still unclear. Assignment tests conducted on rafting reproductive shoots shows that they can have an important role in dispersing genotypes up to 50 km (Reusch, 2002).

5. *Thalassia testudinum*

This species occurs throughout the Caribbean and Gulf of Mexico (Tussenbroek et al., Chapter 18), where periodic die-off of above ground biomass has been observed (Robblee et al., 1991). Studies on genetic diversity among different localities have been conducted using allozymes (Schlueter and Guttman, 1998), RAPD (Kirsten et al., 1998) and AFLP markers (Waycott and Barnes, 2001); microsatellite markers are currently under development (Waycott, unpublished; Kor-Jent unpublished). As for the other species discussed above, a comparison among the results obtained is difficult to make because of differences in the level of genotypic polymorphism detected by the different markers utilized. Eighteen meadows have been sampled in the lower Florida Keys and allozyme analyses show, as expected, low genetic variation within and between sites ($G\text{st} = 0.050$). Although these low values of genetic variability could be due to low inherent polymorphism of the markers, the general trend indicated seems to be real. RAPD and AFLP markers, in fact, also confirm high population connectivity with higher, but still low, within-site genetic variation. In both RAPD and AFLP analyses the partitioning of genetic diversity was distributed similarly, with a higher percent of variation (81.2–96.6%) within meadows. No AFLP differentiation was found between the two regions analysed (overall mean $F\text{st} = 0.03$). In general, *T. testudinum* appears to be a species with weak genetic structure and high homogeneity within its distributional range. The nature of that uniformity is still uncertain, although possibly the result of a recent colonization of the region, following changes in habitat occurring since the Eocene (Waycott and Barnes, unpublished data). Studies on the effects of heavy human impact in the area, the importance of *Thalassia* for the coastal dynamics and more detailed genetic analyses using co-dominant molecular markers (microsatellites) are underway.

6. Other Studies

A modicum of additional information exists on the distribution of genetic diversity in other seagrass species. The introduced species *Halophila stipulacea* has high RAPD diversity in meadows sampled along the Sicilian coasts and high population connectivity between distinct localities (Procaccini et al., 1999a). Absence of clear differentiation in the ITS regions between Mediterranean and Red Sea populations supports the hypothesis of a recent Lessepsian introduction in the Mediterranean (Ruggiero and Procaccini, 2004). The congeneric *H. johnsonii* shows very high clonality and genetic homogeneity in south-eastern Florida, with the same RAPD phenotype present in more than 50% of the samples (Freshwater et al., 2003). In a recent analysis of morphological and genetic variation of *Halophila hawaiiana* (McDermid et al., 2003), no genetic structure was revealed, although the authors utilized a chloroplast DNA homopolymer that may not yield more than species level variability (Waycott and Freshwater, unpublished). *Cymodocea nodosa* seems to occur only as one or few genotypes in Ria Formosa (southern Portugal) (Alberto et al., 2001); whereas, higher genetic variability was found in meadows in the central/southern

Tyrrhenian Sea (Mediterranean Sea) and in the Cadiz Bay, Spain (Atlantic Sea) by means of microsatellite analyses (Alberto et al., 2003b; Ruggiero et al., in press; Ruggiero and Procaccini, unpublished). *Zostera noltii* seems to posses a moderate degree of variability, but very low population connectivity in populations sampled in central/southern Tyrrhenian Sea (Procaccini and Ruggiero, unpublished). Ongoing studies on the complete distribution range of the species are showing significant clustering among distinct geographical regions and high degree of population differentiation at smaller regional scale (Coyer et al., submitted). More data on both *Cymodocea nodosa* and *Zostera noltii* will soon be available using the same markers from several distinct localities inside and outside Mediterranean (Coyer et al., in press). *Halodule wrightii* appears to be distributed in genetically distinct meadows, with high variability, along Texas and Florida coasts (Angel, 2002). *A. antarctica* seems to be represented by a single clone along the whole southern Australian coast (Waycott et al., 1996).

To date, studies generally confirm that patterns of genetic diversity in seagrass species are determined by a series of interconnected factors that are not always easy to distinguish. There is no readily identifiable trend common among species belonging to the same genus, or those theoretically having similar or identical theoretical dispersal capabilities. To more complete understanding of factors causing genetic structure over wide geographical ranges requires the knowledge of local environmental factors, current regimes, human impact and historical colonization events of the area. Difficulties in understanding and predicting population structure often arise from an inadequate knowledge of the factors mentioned above.

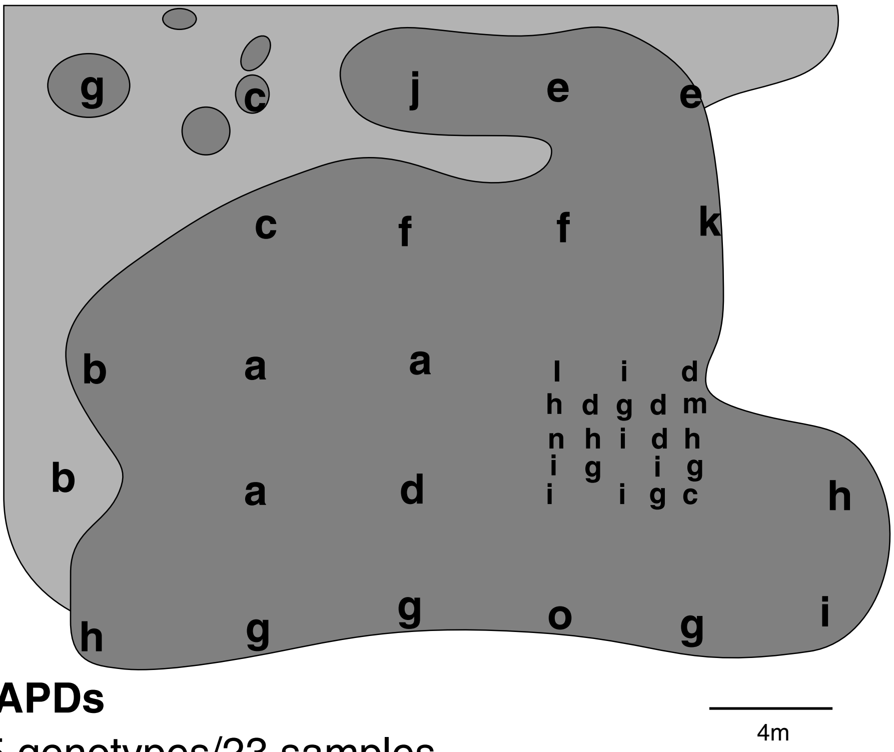
B. Population Structure and Reproductive Strategies

As many of the other chapters in this book will describe, vegetative growth through rhizome extension is a dominant feature of seagrasses. This growth habit allows great flexibility for a single genetic individual to survive in both space and time through clonality resulting from vegetative fragmentation. Most seagrass populations exhibit a mixture of clonal growth along with sexual reproduction and understanding the structure of these populations has proved challenging using standard ecological approaches. The clonal growth form of many seagrass species results in a hierarchy of different organisational levels. The most elementary level of organisation is the ramet (sensu Harper, 1977), the potentially independent individual. In seagrasses, this individual typically is the leaf bundle, a piece of rhizome, and a root bundle (Tomlinson, 1974). Depending on the longevity of rhizome connections between ramets, several ramets can form physiologically integrated clusters, the second level of organization. The size of these clusters varies greatly between species, and may comprise several hundreds of leaf shoots in the genus *Posidonia*. The sexual individual, or genet, are all ramets or ramet clusters which originated from the same zygote. From an evolutionary point of view, it is only the genet that matters and eventually transmits genes to the next generation. Since genets may be exceedingly large, the determination of genet fitness, reproductive output, and longevity poses formidable practical problems. Most ecological studies have ignored the potential genetic identity of leaf shoots or ramets when selecting experimental plants, or plots. Whether or not this has resulted in biased ecological conclusions remains unclear because quantification of heritable differences in ecological performance of clones is lacking in almost all species (but see Hämmerli and Reusch, 2002).

Since physical connections between ramets persist only for a limited time interval, the identification of the ramet/genet organisation in field populations is possible only using genetic markers. While traditional allozyme markers often provide too little polymorphism, modern DNA based molecular markers such as RAPD (random amplified polymorphic DNA), AFLP (amplified fragment length polymorphism) or DNA microsatellites allow precise assignment of leaf shoot samples to ramets and genets based on multi-locus genotypes. As an additional advantage, the Mendelian inheritance of DNA microsatellites allows the calculation of error probabilities for an incorrect assignment of ramets to genets (Reusch et al., 1999d). To date, information on the clonal structure of nine seagrass species is available (*Cymodocea nodosa, Halophila stipulacea, Halophila johnsonii, Posidonia oceanica, Posidonia australis, Thalassia testudinum, Thalassodendron ciliatum, Zostera marina*). In only a few studies were genotypes mapped in space (cf. Waycott, 1995; Kirsten et al., 1998) (e.g. Fig. 7). This

Allozymes

15 genotypes/43 samples



RAPDs

15 genotypes/23 samples

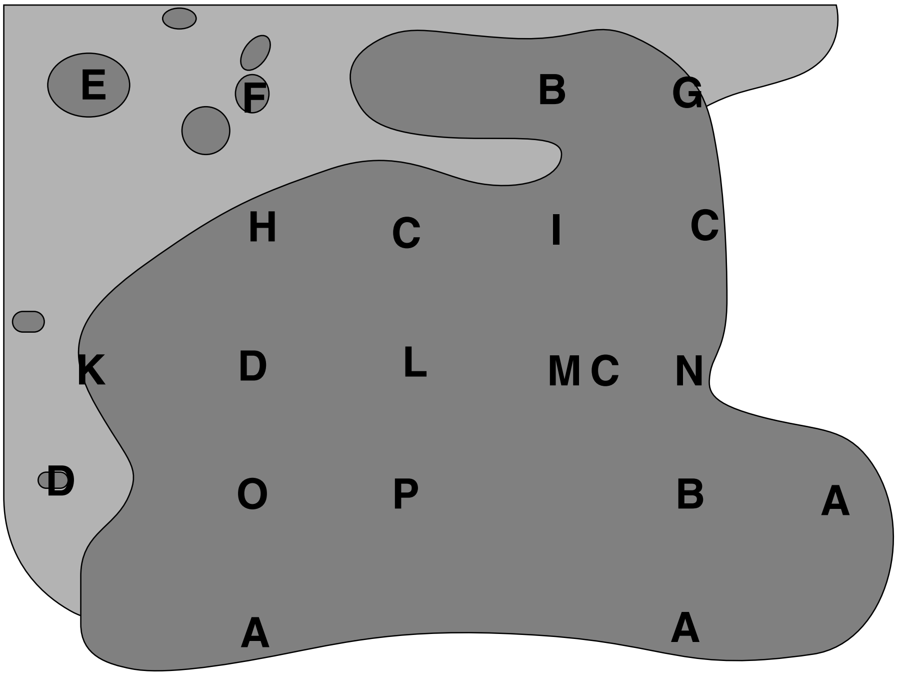


Fig. 7. Clone map of *Posidonia australis* from Western Australia, letters correspond to matching genotypes and are equivalent to ramets of the same clone (from Waycott, 1995).

lack of spatially explicit information is unfortunate as it can be utilized to infer clone sizes age, as well as to characterize the genetic neighborhood of genets within populations (see below).

The large differences in sampling effort, physical distances among samples, and in the resolution of genetic markers employed make comparisons among studies assessing clonal structure difficult. Nevertheless, the use of high-resolution genetic markers has repudiated earlier notions of clonal uniformity in several species, notably *Thalassia testudinum* (Kirsten et al., 1998), *Posidonia australis* (Waycott, 1998) and *Zostera marina* (Reusch et al., 1999d). Previously all three species were thought to comprise only a few clones based on allozyme markers, while DNA based markers revealed several distinct genotypes at the m-scale.

A second major finding was that a widely varying degree of clonal diversity occurs among locations within species. For example, in *Posidonia oceanica*, there are sites in the Adriatic Sea with only a single detectable genotype (Ruggiero et al., 2002); whereas, other populations in more central areas of the Mediterranean are multi-clonal (Procaccini et al., 2001). A similar range in clonal diversity has been observed in the Australian species *Posidonia australis* (Waycott, 1998). The northern-temperate species *Zostera marina* shows an even wider range of clonal diversity across locations, from monoclonal stands to populations where each genotype is unique (Reusch et al., 2000).

The causes of widely varying clonal diversities across locations and species are largely unknown. The proximate reason for the variation observed is probably a shift in the relative success of sexual vs. vegetative reproduction. Although almost nothing is known regarding how variation in reproductive output in seagrass populations translates into rates of successful recruitment, some evidence points to extrinsic forcing favouring sexual recruitment. There is limited evidence from eelgrass (*Zostera marina*) that clonal diversity is higher at sites with greater physical disturbance (Hämmerli and Reusch, 2003b). This is a plausible scenario because the chances of establishment in closed seagrass canopies are low, while gaps may facilitate the emergence of seedlings and hence, new genotypes to the local population (Eriksson and Fröborg, 1996). A recent study by Hämmerli and Reusch (2003b) also found that genotypes with a higher individual heterozygosity, measured at nine polymorphic DNA microsatellite loci, were larger on average than more inbred clones. Over time, clonal competition seems to favour those genets, which have a higher genetic diversity at the level of individuals. Thus, the local diversity and size distribution of clones also has a deterministic component.

Populations at the distribution limit may also reveal low clonal diversity because sexual reproduction at marginal sites may be reduced or even completely prevented ('geographic parthenogenesis' of Bierzychudek (1985). Such a scenario may apply to seagrasses. For three different seagrass species findings from DNA based markers indicate that populations at the distributional margin may consist of very large clones [*Cymodocea nodosa*: (Alberto et al., 2001); *Posidonia oceanica*: (Ruggiero et al., 2002); *Zostera marina*: (Reusch et al., 1999a); or possess significantly reduced genetic diversity as in *Posidonia australis*: (Waycott et al., 1997)]. As a corollary, successful sexual reproduction at entirely clonal sites may be practically undetectable, although it must have occurred at one point in time if we are not to invoke re-establishing of rafting vegetative fragments as an explanation. Clearly, much more experimental work at the within-population scale, coupled with censuses at the geographic scale are needed to explain extent and variation in clonal diversity among seagrasses, both at the species, and the population level.

The clonal life-history strategy has important ramifications for processes within populations (see Duarte et al., Chapter 11), in particular for the mating system. In the centre of large clones, focal ramets may be surrounded by members of the same clone (Handel, 1985). In monoecious (*Zostera* spp.) and hermaproditic (*Posidonia* spp.) seagrass genera, the opportunity for outcrossing is thus constrained by the spatial architecture of the genets in a meadow. Not surprisingly, seeds in focal flowering shoots in monoecious *Zostera marina* show selfing rates up to 65% due to between-ramet geitonogamy when growing in a selfing neighborhood (Reusch, 2001a). Selection against selfed progeny effectively restores Hardy-Weinberg-equilibrium in the adult population. Since fitness costs associated with inadvertent between ramet selfing are substantial (Ruckelshaus, 1995; Reusch, 2001a), these findings may provide one possible explanation for the evolution of dioecy in seagrasses. Evidently, within-clone selfing is impossible in dioecious seagrasses, as there are separate male and female plants. However, the high incidence of dioecy may also reflect the sexual conditions of monocotyledonous plants ancestral to seagrasses (Waycott and Les, 1996; Les et al., 1997).

Long-term demographic censuses are often unavailable for many seagrass populations. Unravelling the spatial pattern of ramets and genets in a seagrass meadow uncovers parts of its local demographic history. Hence, as a potential alternative to census data, important demographic information may be inferred from a genetic analysis of the spatial arrangement of clones. For example, the detection of identical multi-locus genotypes among distant vegetation patches may indicate the fragmentation of previously continuous meadow. Moreover, minimal estimates of meadow age can be inferred from rates of lateral spread of clones in conjunction with the aerial extension of clones (Reusch et al., 1999d). In several northern Baltic Sea populations of *Zostera marina*, vegetation patches are composed of shoots with one identical genotype (TBH Reusch and C. Boström, unpublished data), suggesting that the initiation of patches often starts with a single seedling.

Within-population genetic structure not only comprises the ramet–genet dichotomy but also involves the dispersal capability of pollination and sexual progeny. Given that seeds and pollen are thought to typically travel only a few meters (Ruckelshaus, 1996) (but cf. Harwell and Orth, 2002), germinating seedlings will often be related genetically to nearby plants. Thus, additional population structure can be expected at the scale of meters. Spatial autocorrelation techniques are a powerful tool to detect such structure (Heywood, 1991). In autocorrelation analyses, the genetic similarity among pairs of ramets is analysed as a function of their pairwise distance. If autocorrelation values are positive, genetic relatedness is higher as expected under random mating, and *vice versa*. As clonal plants, seagrasses require special attention because the inclusion of members of the same clone into an autocorrelation analysis inflates small-scale kinship structures (Reusch et al., 1999b). In a recent study using a high-resolution spatial sampling grid (Hämmerli and Reusch, 2003a), a significant positive spatial autocorrelation in kinship coefficients was found at distances between 2 and 5 m even when counting each clone only once. Significant positive spatial autocorrelation was also found between 1 and 11 m in *Cymodocea nodosa* and between 2 and 7 m in *Zostera noltii* (Ruggiero and Procaccini, unpublished). Thus, for any focal shoot, the landscape of neighbouring plants is complex and consists of several levels of genetic sub-structuring. Clone affiliation, clone spatial arrangement and local kinship patterns interact to influence mating patterns, clonal competition and reproductive output in apparently homogeneous seagrass meadows.

C. Mating Systems

Plant mating systems are one of the most significant factors in the transmission of genetic diversity between generations (Clegg, 1980). The measurement of plant mating systems is complicated since an overwhelming majority of angiosperm species possess both male and female flowers on the same plant (Richards, 1997). These bisexual plants are therefore capable of self-pollination either from the same flower (autogamy) or separate flowers on the same plant (geitonogamy). Most seagrass species are dioecious (individuals of separate sex) (Waycott and Les, 1996; Les et al., 1997) and as such cannot self pollinate. However, even dioecious plants can be subject to inbreeding through the mating of siblings or parent-offspring. In this context, two components of seagrass mating systems are particularly significant, first the movement of pollen between flowers within a meadow and second the genetic structuring of plants within populations as described in the proceeding section.

Sexual reproduction in the marine environment is limited by the ability of pollen to reach stigmas (Pettitt et al., 1981; Cox, 1988; Ackerman, 1995; Verduin, 1996; Reusch, 2003; Ackerman, Chapter 4). Seagrass pollination occurs by hydrophily, that is, water mediated, abiotic pollination (Fægri and van der Pijl, 1979). Our understanding of pollination in seagrasses is limited by the interaction of the timing of pollen release/capture and the hydrodynamic environment in which these events occur. A correlation between hydrodynamic environment and the efficiency of pollen movement between flowers, and thus outcrossing, has been proposed by Waycott and Sampson (1997) for *Posidonia australis*. However, the spatial arrangement of flowers in a seagrass meadow is critical to the outcome of any mating event as the greater the area a flowering genet covers the greater the chance there will be self-pollination as found by Reusch (2001a) where outcrossing rate was positively correlated with clonal diversity (Fig. 8). For example in populations of Northern European *Zostera marina*, pollen limitation has been

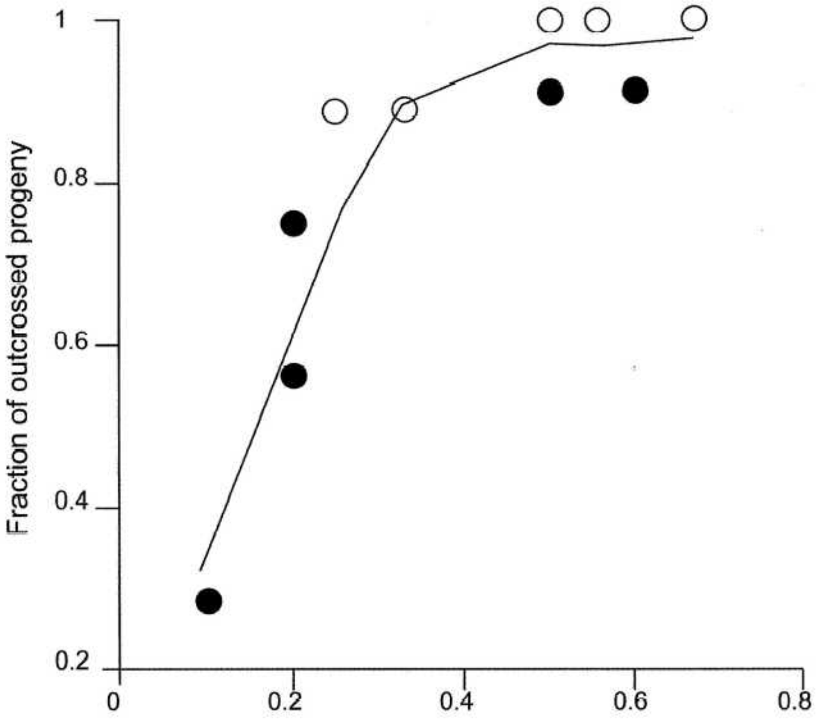


Fig. 8. Relationship between clone number per patch of seagrass and outcrossing rate in *Zostera marina* from two populations in northern Europe (redrawn from Reusch, 2001a).

experimentally demonstrated in a field experiment, where decreased seed set when the density of flowering shoots was below 5 shoots m^{-2} (Reusch, 2003). Interestingly, *Zostera marina* adjusts its instantaneous sex ratio (i.e. the ratio of male to female flowering stages) as to maximize the chances to receive outcrossing pollen, as demonstrated in a mesocosm experiment. This way, the negative effects of a monoclonal genetic neighbourhood on the outcrossing rate can be minimized (Hämmerli and Reusch, 2003c).

Assessment of plant mating systems is primarily done in bisexual species as the analyses detect the genotype of the ovule donor (maternal genotype) and document the number of times genetic information must have been derived from a non-maternal source. Detection of inbreeding among related individuals in a dioecious species, although possible, is difficult as the detection of relatedness requires large sample size and fine scale analysis of genetic relatedness. Thus, among the seagrasses we are limited to assessing the mating system (i.e. frequency of selfing) of only three genera: *Posidonia*, *Zostera* and two species of *Halophila*. It is also extremely difficult to estimate outcrossing rates from non-codominant markers although there have been attempts to do so in other plant species (e.g. Krauss, 1999). Thus, studies are usually limited to those markers that detect codominant genotypes as alleles present in both ovule donor and pollen donor such as allozymes and microsatellites (SSRs).

To date, mating system studies, or those that utilize outcrossing estimates, have been conducted for *Zostera marina* (Ruckelshaus, 1995; Ruckelshaus, 1996; Ruckelshaus, 1998; Reusch, 2000; Reusch, 2001a; Hämmerli and Reusch, 2003b), and *Posidonia australis* (Waycott and Sampson, 1997). In *Zostera marina*, outcrossing rates (t) are usually high (t; 0.61–0.97); however, estimates using microsatellite markers were higher than allozyme markers as would be expected given the increased sensitivity of the DNA marker system (Reusch, 2001a).

The normally high outcrossing rates in *Zostera marina* are reduced in populations where there are fewer clones per patch (Reusch, 2001a). Conversly, genetic diversity of *Posidonia australis* populations did not have an effect on the outcrossing rate

(Waycott and Sampson, 1997) although the exact structure of the population sampled for mating system analysis was not documented. It should be noted however that a large proportion of seagrass populations studied to date have mixed population structure (see proceeding sections this chapter) and in such populations there will be a high probability that seed production will result from outcrossing in these populations. However, it is important to document fine scale population structure alongside the mating system in seagrasses to fully appreciate the implications of any measurement of outcrossing (or by implication inbreeding). In addition, the hydrodynamics of pollen movement needs to be understood better to account for pollen movement and the interaction of the biotic and abiotic factors affecting successful sexual reproduction (Cox et al., 1992; Verduin, 1996; Ackerman, 1997).

Mating system estimates provide a more detailed understanding of population processes such as small scale gene flow, the frequency of inbreeding and estimates of inbreeding depression (e.g. Ruckelshaus, 1995; Hämmerli and Reusch, 2003b). The consequences of inbreeding can significantly impact a species primarily due to reduction in progeny fitness (Charlesworth and Charlesworth, 1987; Ellstrand and Elam, 1993). For this reason alone, estimates of inbreeding are valuable and should be obtained for a greater range of seagrass species.

IV. Concluding Remarks

A. Inferences for Ecology, Conservation and Rehabilitation

Outcomes from population genetic analysis can substantially influence the way we perceive how seagrass ecosystems interact and can identify where important reservoirs of genetic diversity may exist. Different scales of gene flow can be very important for assessing the real significance of geographic isolation and habitat fragmentation in the context of protecting and managing seagrass meadows. Many recent results suggest that seagrasses are capable of at least some long distance dispersal (e.g. Reusch et al., 2000; Waycott and Barnes, 2001; Les et al., 2002; Reusch, 2002; Waycott et al., 2002). These results based on broader scale population genetic and phylogeographic studies imply that the perception of seagrasses as isolated disconnected populations requires reassessment. Considerable insight will be gained from studies that explore these processes using both an ecological and genetic approach. In addition to the outcomes for an improved understanding of population ecology such studies enhance our ability to reconstruct historical processes that have lead to isolation of populations.

Determining population genetic isolation is particularly important for defining correct strategies for collecting transplants to re-establish lost seagrass meadows, a practice now widespread (Fonseca et al., 1998). Broad scale studies identify areas with lower genetic diversity and lower exchange with other localities. The definition of genetic distinction among populations facilitates selection of appropriate donor beds for transplantation programs, according to their relative levels of polymorphism and genetic distinctiveness. In such studies, genetic diversity needs to be carefully defined, as it has two levels in seagrasses, genotypic diversity and genetic diversity. Previous studies were often unable to distinguish between both levels since markers were not polymorphic enough. However, this may be critical when selecting donor beds. For example, a few large heterozygous clones may be ideal starting material for transplantations, yet they could be assessed as genetically uniform when clonal diversity cannot be separated from genetic diversity. A transplant study on *Posidonia oceanica* has suggested, in fact, that transplants coming from genetically polymorphic populations have a greater probability of survival and perform better in common garden experiments (Procaccini and Piazzi, 2001). In addition, understanding the genetic consequences of transplantation may allow us to better infer the ability of those beds to survive in longer time frames (e.g. see Williams, 2001).

B. Interactions of Scale and the Appropriate Use of Molecular Markers

The preceding sections of this chapter present a broad range of scale in genetic analyses of seagrasses from phylogenetic relationships at the subclass level to centimetre scale measures of gene flow. The interpretation of processes should be made with these differences in scale in mind. For example, it is clear that *Zostera marina* represents a distinct evolutionary lineage to the southern hemisphere *Zostera* species based on molecular phylogenetic results (Les et al., 2002). However, these analyses were done with relatively few individuals sampled for each species as is appropriate for phylogenetic analysis. In comparison, fine scale estimates of inbreeding and population structure within populations in Europe and the USA have provided insight into the interaction between ecology and evolutionary strategies in this species (Ruckelshaus, 1998; Williams and Orth, 1998; Reusch et al., 1999d; Reusch, 2001a; Olsen et al., 2004). However, the connection between the broadest scale process and the evolution of this species is only now being revealed through studies using high resolution, species-wide population genetic analysis (Olsen et al., 2004).

Thus, a significant issue in the interpretation of genetic data are the level of diversity detected using particular genetic markers. This issue has been exemplified in the early studies that utilized allozymes to detect genetic diversity (e.g. McMillan, 1991) and which revealed very high levels of genetic homogeneity (see Les, 1988 for discussion). Although subsequent studies on the same species using allozymes revealed significantly greater polymorphism than early studies (Ruckelshaus, 1995; Waycott, 1995; Ruckelshaus, 1996; Waycott et al., 1997; Waycott and Sampson, 1997; Ruckelshaus, 1998; Waycott, 1998), DNA based markers revealed even higher levels of variability (Waycott, 1995; Waycott et al., 1996; Waycott, 1998; Reusch et al., 1999d; Reusch et al., 1999c; Reusch et al., 2000).

New approaches are being developed continuously that allow improved interpretations of the different hierarchical processes of interest (e.g. Zhang and Hewitt, 2003). For example, there is now a growing interest in studying adaptive genetic polymorphism at the DNA level. To undertake such studies, however, polymorphism in genes of adaptive significance must be analysed. There are a number of candidate genes to begin these studies, for example genes related to photosynthesis (García-Gil et al., 2003) or to heat stress (Heckathorn et al., 1996), which can be inferred from model plants. Marker loci provide one view on the measurement of genetic diversity; the future of many genetic studies will be to understand the effects, polymorphism and fitness consequences of loci that selection will actually operate upon (see, for example, Mitchell-Olds, 2001 and references therein). It is therefore worthwhile to invest in the most variable and informative marker (currently microsatellite markers for population analyses and DNA sequences of multiple loci for phylogeny) available within the constraints of time and budget for a project.

To ensure adequate future survival of seagrasses, globally, a greater understanding of the relationships between species, the baseline genetic variability of species, their reproductive biology and unique adaptive traits is needed and such knowledge will become increasingly available, as discussed in this chapter.

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Chapter 3

Seagrass Morphology, Anatomy, and Ultrastructure

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I. Introduction

Seagrasses possess similar organs and tissues as the other flowering plants. Nearly all-mature flowering plants have distinctive above and below ground parts. The exceptions are some pleustophytes such as the Lemnaceae and representatives of the genus *Ceratophyllum*, and haptophytes such as the Podostemaceae. Below ground parts normally consist of roots for anchoring and rhizomes/stems for mechanical support. Above ground parts usually constitute shoots bearing several leaves. A leaf usually has a basal sheath for protecting the apical meristem and developing leaves, and a distal blade for producing food by photosynthesis and giving off water vapor through transpiration. All organs consist of three basic tissues with a different structure and function: (a) The epidermis forms a continuous layer on the surface of the plant body and has a cuticle on the outer wall to provide mechanical protection, and restricting transpiration and aeration; (b) The vascular bundle contains the phloem for solute translocation and the xylem for water transport; (c) The parenchyma tissue with thin walls and non-lignified collenchyma is responsible for photosynthesis and storage and the thick walled lignified sclerenchyma acts as a mechanical support. An air space system allows movement of gases through the plant. During the reproductive period, flowering plants produce flowers for pollination and fertilization and then to set seeds to complete their life cycles.

In contrast to terrestrial monocotyledons, seagrasses have to live in marine or highly saline environments, and this has profoundly influenced their morphology and anatomy. This chapter will examine how tissues and organs of these unusual plants in both vegetative and reproductive phase have been modified to allow them to complete their life cycle in the marine environment.

Sauvageau (1890, 1891) provided the first basis for our understanding of the vegetative anatomy of seagrasses through excellent descriptions and illustrations. Arber (1920) surveyed the older morphological and anatomical literature of aquatic plants and Sculthorpe (1967) further advanced the knowledge of the ecology and biology of herbaceous aquatic plants. den Hartog (1970) established the boundary of modern seagrass taxonomy with precise morphological characters. Tomlinson (1982) reviewed old literature and further documented general morphology, detailed anatomy of vegetative organs and sometimes also reproductive structures in each genus of the helobian monocotyledons, including seagrasses. He also specifically discussed leaf morphology and anatomy in relation to taxonomy in seagrasses (Tomlinson, 1980). Kuo and McComb (1989) provided a review of the structure and function, mainly of vegetative organs by combining morphological, anatomical and ultrastructural data. McConchie and Knox (1989a) added similar information on reproductive biology and pollination in seagrasses. The earlier morphological and anatomical scientific data which have been discussed previously (e.g. Tomlinson, 1982; Kuo and McComb, 1989; McConchie and Knox,

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1989a) will not be dealt with again in this review, unless essential. The taxonomic arrangement of the seagrasses as given by den Hartog and Kuo, Chapter 1, is used in this chapter.

II. General Morphology of Seagrasses—Size and Shape

Seagrasses are herbaceous plants (although stiff and hard upright stems and rhizomes do occur), and can be grouped into three main morphological categories with some taxonomic implications.

a. Plants without strap-shaped leaves but with either a pair of petiolate leaves at the rhizome node or two or more leaflets on each of the distal nodes of the erect stem. This category is restricted to *Halophila*, which has the smallest shoots among seagrasses. Shoots can be less than 1 cm in length, as for *H. beccarii* and *H. minor* (Fig. 1B and C), and up to 20 cm long as for *H. australis*.
b. Shoots with a distinct erect stem and strap-shaped leaves borne at the top of an erect stem. This group includes *Thalassia* of the Hydrocharitaceae and all genera of the Cymodoceaceae (Fig. 1F and I).
c. Plants without visible erect stems, but with strap-shaped leaves derived from the rhizome nodes. *Enhalus* of the Hydrocharitaceae, the Posidoniaceae and all members of the Zosteraceae belong to this group (Fig. 1A, D and E). The leaves of some members of *Zostera* subgenus *Zosterella* can be as small as 10 cm; while for *Enhalus, Posidonia, Zostera* subgenus *Zostera* and *Phyllospadix*, it is not uncommon for them to reach 1 m or more.

Vegetative organs of all seagrasses have a well-developed creeping rhizome. At each node or at certain nodes there are one or more branched or unbranched roots and a shoot or an erect stem bearing several leaves.

III. Vegetative Morphology and Anatomy

A. Roots

1. Root Morphology

The roots of seagrasses are adventitious and arise from the lower surface of the rhizomes, generally at the nodes. The external morphology of roots often has characteristic features in different genera, which do not necessarily completely relate to specific types of substrates. For example, *Enhalus* bears several coarse, soft, unbranched roots with a few short root hairs (Fig. 1A), and grows on muddy substrata. In contrast, both *Thalassia* and *Halophila* (Fig. 1B) produce unbranched roots with massive root hairs for penetrating various types of substrata. Roots of *Zostera* and *Heterozostera* in the Zosteraceae are always arranged in two groups, each bearing 2–12 unbranched, slender roots with numerous long root hairs (Fig. 2A, B and J) for growing in muddy to sandy substrata. On the other hand, roots of *Phyllospadix* also occur in two groups at rhizome nodes, but they are extremely short and covered with dense root hairs, together with robust rhizomes (Fig. 2L–N). Unlike other seagrasses, *Phyllospadix* can firmly attach to rock surfaces in high-energy environments (Cooper and McRoy, 1988; Barnabas, 1994b). The roots of *Posidonia* are thick, soft and extensively branched (Fig. 1E), but root hairs are rare (Fig. 2F), and are usually associated with sandy substrata. The Cymodoceaceae including *Syringodium, Cymodocea* and *Halodule* have, at each rhizome node, one or more moderately branched roots with few root hairs (Figs. 1F–H and 2D); they usually grow on coral sands. The roots of *Amphibolis* are wire-like and moderately branched, with no root hairs, while those of *Thalassodendron* are woody, thick and strong with a shiny black surface, rarely branched, with a few short root hairs only near the root tip (Figs. 1I and 2C and E). In general, *Amphibolis* and *Thalassodendron* are associated with firm sedimentary and, sometimes, rocky substrata; the roots of *Thalassodendron* can penetrate the gaps in hard calcareous reef floors.

2. Root Anatomy and Ultrastructure

The root tip of all seagrasses has a distinct root cap protecting meristematic cells, which provides a continuous set of dividing cells. The mature region may bear root hairs depending on the species and overlying cortical parenchymatous tissues, which enclose air lacunae and a central stele. However, the details of root anatomy may be different among seagrass groups reflecting their root morphology and the substratum.

On the outer-most layer, the epidermal cells usually have thin, unlignified walls and a peripheral cytoplasm. The walls of these cells are soft in

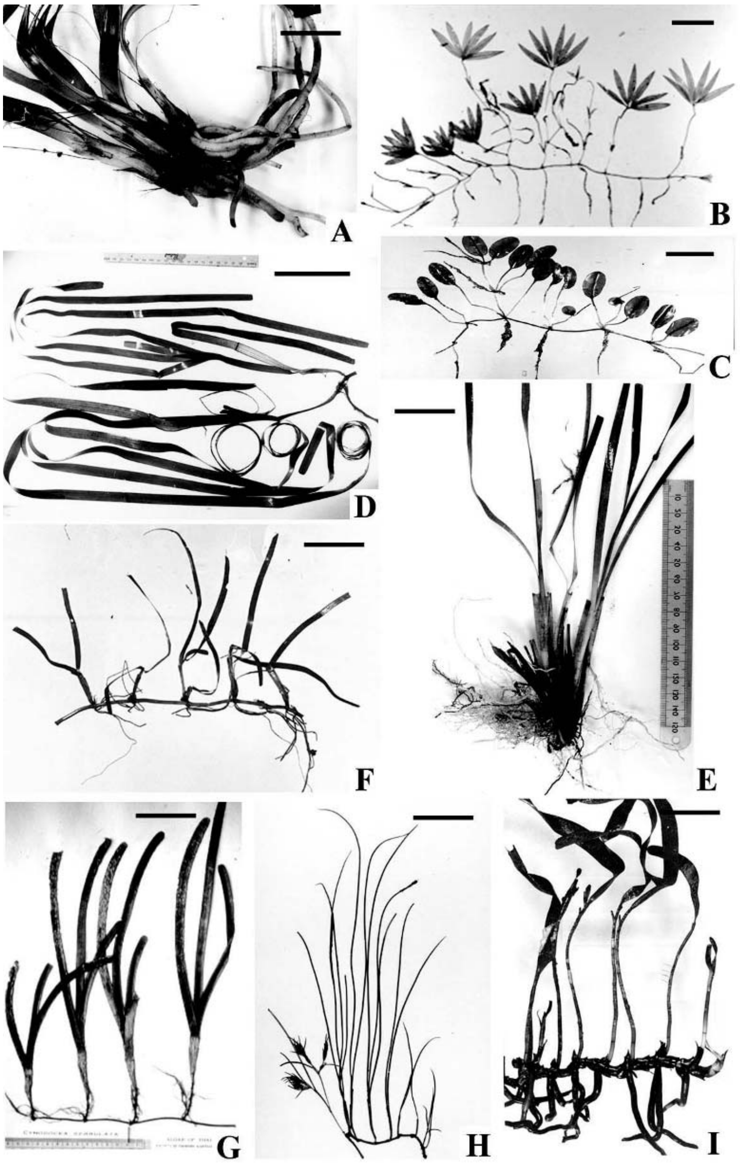

Fig. 1. General morphology of seagrasses. A. *Enhalus acoroides*. Scale = 3 cm. B. *Halophila engelmanni*. Scale = 3 mm. C. *Halophila minor*. Scale = 2 cm. D. *Zostera asiatica*. Scale = 15 cm. E. *Posidonia sinuosa*. Scale = 3.5 cm. F. *Halodule uninervis*. Scale = 2.5 cm. G. *Cymodocea serrulata*. Scale = 5 cm. H. *Syringodium isoetifolium*. Scale = 4.5 cm. I. *Thalassodendron pachyrhizum*. Scale = 4 cm.

Posidonia and *Syringodium* whose roots are thin and lignified (Fig. 3A), but cell walls in the hard roots of *Thalassodendron* and *Amphibolis* are thickened and lignified. Inside the epidermis, there is a distinct exodermis of one or more cell layers, each of which has thickened but unlignified walls containing suberin lamellae (Fig. 3C) (see Kuo and McComb, 1989; Kuo, 1993b). Exodermal cells in roots of *Thalassodendron* and *Amphibolis* are thickened and lignified (Kuo, 1983). Barnabas (1994b, 1996) showed that the Casparian strip-like structure of the exodermis was also present in other aquatic plants including the seagrass genera *Zostera* (Fig. 2I), *Halodule* (Fig. 3B), *Halophila*, the brackish-water genus *Ruppia*, and even the freshwater species of *Potamogeton* and *Nymphaea.* The exodermal cells abutting root hairs of *Zostera capensis* (Barnabas and Arnott, 1987) show the characteristics of transfer cells (Gunning and Pate, 1969; Gunning, 1972; Pate and Gunning, 1972). In contrast, walls between

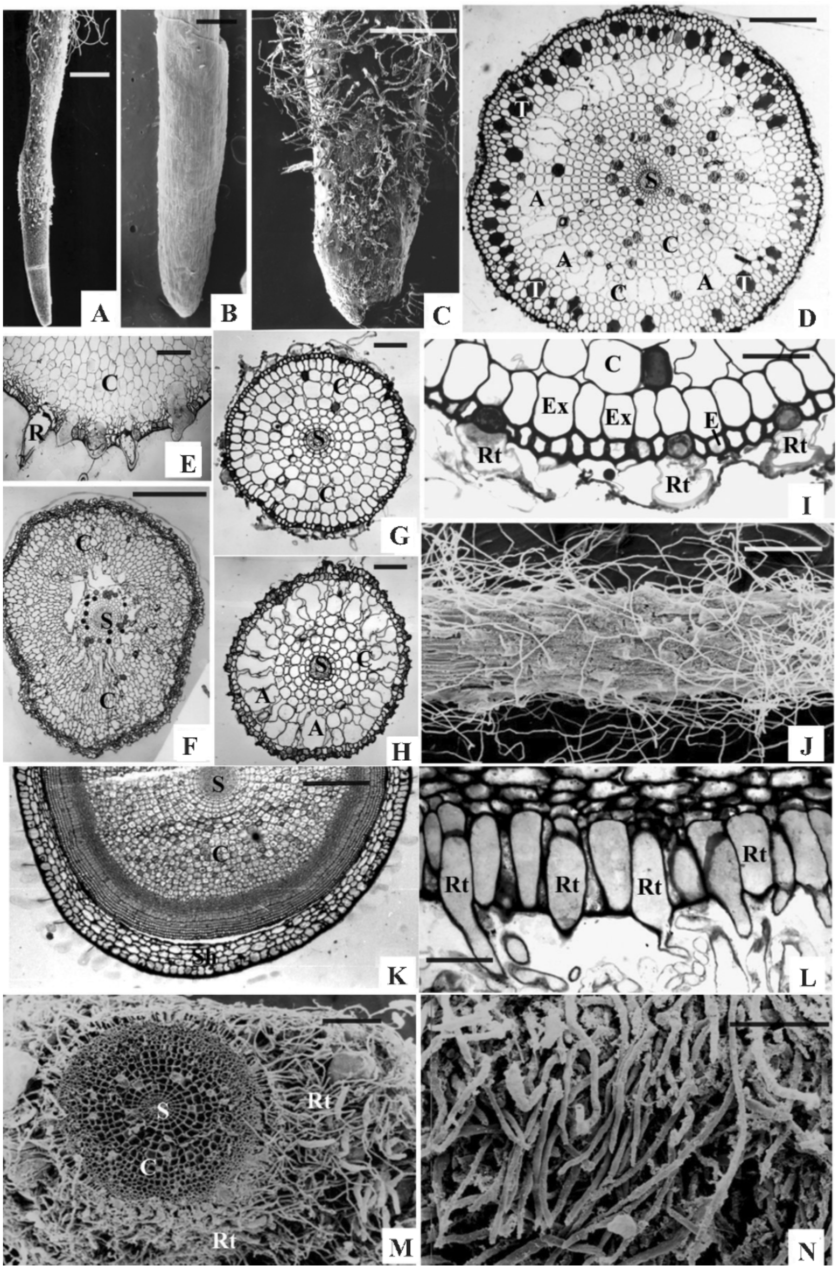

Fig. 2. Morphology and anatomy of roots. A. *Zostera caespitosa*. Root hairs normally are produced some distance from the root tip. Scale = 500 µm. B. *Zostera marina*. A root cap protects the root tip. Scale = 160 µm. C. *Thalassodendron pachyrhizum.* Relatively thick hairs are produced near the root tip. Scale = 1 mm. D. *Cymodocea rotundata*. The root has a small stele (S) and a large cortex (C), which has three distinct regions. The outer and inner cortexes have smaller cells, some of which contain tannin substance (T), while the middle cortex has large air lacunae (A). Scale = 300 µm. E. *Thalassodendron pachyrhizum*. Sparse but rather thick root hairs (R) are produced. Scale = 140 µm. F. *Posidonia sinuosa*. The division of cortical tissues (C) is not distinct. Some tannin substances occur near the stele (S). Scale = 500 µm. G, H. *Zostera japonica*. A simple cortical tissue (C) is surrounding the central stele (S) near root tip (G), while large air lacunae (A) form in the mature root region (H). Scales = 200 µm. I, J. *Zostera marina*. Root epidermal cells (E) are small and have thick cell walls, some of these cells produce root hairs (Rt). Scales I = 40 µm, J = 300 µm. K. *Phyllospadix scouleri*. Differentiating root tissues near root tip. Note a rather complex peripheral region. Scale = 300 µm. L, M. *Phyllospadix japonica*. Each epidermal cell produces a root hair (Rt). Scale L = 100 µm, M = 2 mm. N. *Phyllospadix iwatensis*. Dense short root hairs. Scale = 50 µm.

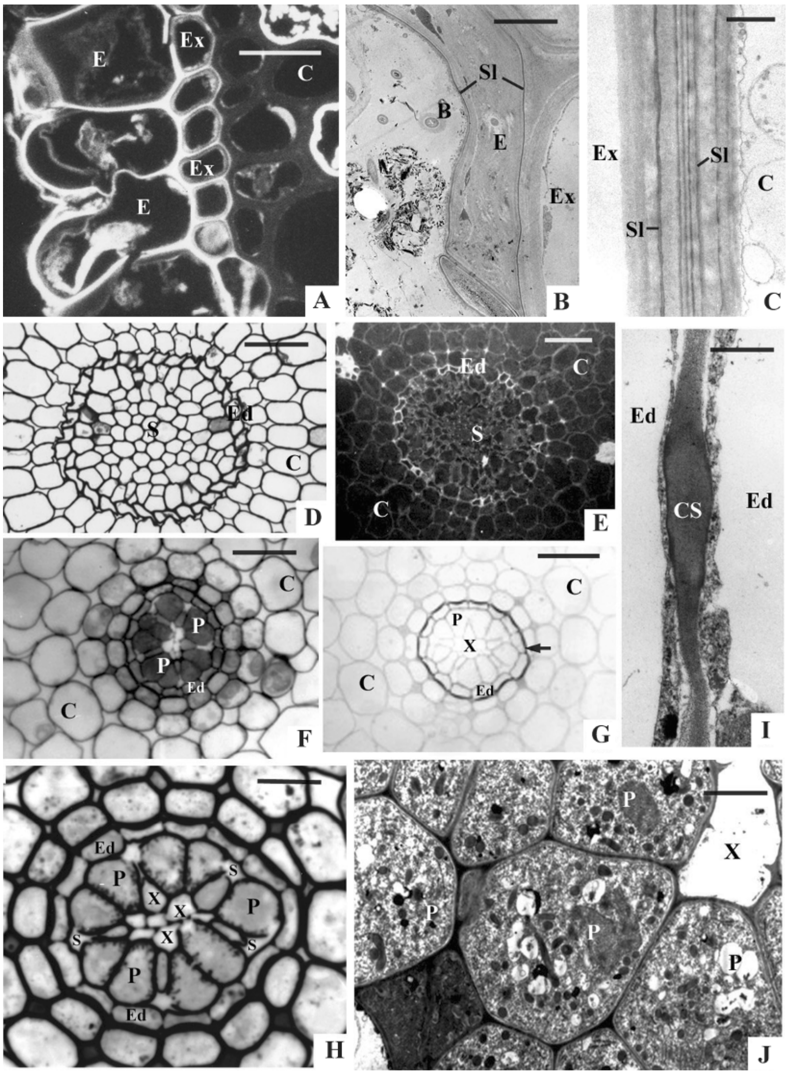

Fig. 3. Anatomy and ultrastructure of roots. A. *Syringodium isoetifolium*. The walls of epidermal (E) and exodermis (Ex) are lignified and autofluorescent, while those of cortical cells (C) are not. Scale = 25 μm. B. *Halodule uninervis*. The cell walls of epidermal cells (E) possess a thin electron dense suberin layer (SL). Some bacterial colonies (B) also occur in the rhizosphere. Scale = 4 μm. C. *Amphibolis antarctica*. Suberin layers (SL) occur in the walls of both exodermal (Ex) and cortical cells (C). Scale = 1 μm. D. *Cymodocea nodosa*. The central stele (S) is surrounded by a distinct layer of the endodermis (Ed), which is located in the inner most layer of cortical tissue (C). Scale = 50 μm. E. *Posidonia australis*. The cell walls of the endodermis (Ed) are slightly thickened and more autofluorescent than those of cells in the central stele (S) and cortical cells (C). F. *Zostera marina*. The endodermis (Ed) is surrounding a group of large parenchyma cells (P) and the central xylem elements (x). Amido black stained. Scale = 30 μm. G. *Zostera marina*. The outer walls (arrow) of the endodermis (Ed) are strongly stained with Sudan black, while those of parenchyma cells (P), xylem elements (x) and cortical cells (C) are not. Scale = 30 μm. H. *Zostera marina*. Several small sieve tubes (s) occur between the endodermis (Ed) and parenchyma cells (P). Few xylem elements (x) are present in the central stele, Casparian strips in radial walls of the endodermis are weakly stained. Scale = 150 μm. I. *Posidonia australis*. Casparian strip (CS) occurs in the radial walls of the adjacent endodermis (Ed). Scale = 0.3 μm. J. *Phyllospadix iwatensis*. Organelle-rich stele parenchyma cells (P) adjacent to xylem elements (X). Scale = 10 μm.

the exodermal cells and root hair producing epidermal cells in *Halophila ovalis* do not have wall ingrowths, but possess numerous plasmodesmata (Roberts, 1993). Both wall ingrowths and plasmodesmata in the exodermal cells may play a similar role in nutrient uptake by root hairs, and transfer this nutrient into the cortical cells. Furthermore, Webster and Stone (1994a) reported that the walls of root hairs in *Heterozostera nigricaulis* (as *H. tasmanica*) contain cutin or lipid, callose (1–3) β-glucans, carbohydrates but no lignin. The major wall polysaccharide is an apiogalacturonan and that cellulose accounts for most of the glucose.

Cell structure and the arrangement of the cortex varies with the texture of root types, but roots always have three distinct zones. In soft roots, such as those of *Posidonia* (Fig. 2F) and *Halophila*, the outer cortex consists of one to several layers of compact cells with thin, non-lignified walls. The middle cortex has well developed air lacunae separated by a radial partition, which is one cell thick, containing small intercellular pores, and the inner cortex consists of compact, small cells in a regular, concentric arrangement (Roberts et al., 1985; Kuo and McComb, 1989; Kuo, 1993b). On the other hand, in hard roots such as those of *Thalassodendron* (Fig. 2E) and *Amphibolis*, the outer cortex consists of several compact cells with slightly thicker, lignified walls. The middle cortex contains several layers of thin-walled, irregular cells in two or more layers that sometimes make up some distinct but irregular air lacunae (Fig. 2D and H). The inner cortex has two or more layers of small, thin walled, compact cells (Figs. 2D–H, K and M and 3D–H). These pronounced air lacunae may facilitate gas movement from the root surface to the stele or *vice versa* and also from the root base to the root tip (Tomlinson, 1982; see also Borum et al., Chapter 10). In all seagrass species, the very distinct endodermis consists of a layer of compact cells, which encloses the stele, as is also the case in many terrestrial plants (Fig. 3D–H). In all species, the walls of the endodermis are thin to moderately thick, either lignified or not lignified, but they always contain a distinct Casparian strip on the radial walls (Fig. 3I). An additional suberized layer may occur in all walls or certain walls of the endodermis of some species (Fig. 3G). The endodermis of seagrasses just as in terrestrial flowering plants restricts solute and water movements between the cortex and the stele (Kuo and Cambridge, 1978). The stele contains the vascular tissue with xylem and phloem but no distinct pericycle (Fig. 3H). Xylem elements are either represented by a few, unthickened walls of poorly lignified tracheid elements or by a single large lumen (Fig. 3F–H). Several sieve tubes with normal walls are surrounded by vascular parenchyma cells (Fig. 3H); these possess wall ingrowths and are rich in cytoplasm in *Zostera* (Fig. 3H and J) (Barnabas and Arnott, 1987).

Tomlinson (1969) studied the development of roots of *Thalassia testudinum* and concluded that there were no water-conducting tissues, except close to the base of the root, suggesting that roots were of no special significance in water absorption in this species. On the other hand, Roberts et al. (1985) found that in the developing roots of *Halophila ovalis*, sieve tubes are differentiated before xylem elements and the formation of root hairs; Casparian strip formation and xylem differentiation were approximately synchronous. These findings suggest that all root structures in *H. ovalis* are involved in the uptake and transport of materials.

Roberts (1993) showed that 39% of root epidermal cells in *H. ovalis* produce root hairs resulting in an increase in the effective root surface by 215%. Furthermore, epidermal cells that produced root hairs contained more cytoplasm and had a greater number of plasmodesmatal connections with the underlying outer cortical cells than adjacent cells that did not produce root hairs (Roberts, 1993). These observations suggest that epidermal cells that produce root hairs play a more active role in nutrient uptake and exchange than other epidermal cells in *H. ovalis*.

In addition to their anchoring function, seagrass roots have other biological functions such as nutrient uptake from the substratum and providing a suitable environment for microorganisms in the rhizosphere. As in terrestrial monocotyledons, both suberized walls and Casparian strips in exodermis and endodermis can restrict water and solutes transport in seagrass roots (Kuo and McComb, 1989).

The rhizosphere of many seagrasses has been found to support a diversity of microorganisms, especially bacteria. They occur mainly on the root surface; tissue penetration rarely occurs, and then only into the periphery of the host (Kuo and Cambridge, 1978; Kuo et al., 1981; Cambridge and Kuo, 1982, Kuo, 1993b). Nielsen et al. (2001) reported that bacteria patchily colonize 1–3% of the surface area of roots and rhizomes of *Zostera noltii*. Nitrogen fixation associated with roots and rhizomes in this species accounts for 31% of the nitrogen fixed in the rhizosphere of *Z. noltii*. In addition, plant-associated nitrogen fixation could supply 37–1613% of the nitrogen needed by the sulfate-reducing community (for further discussion see Marbà et al., Chapter 6).

Fungi were found to have penetrated the epidermal cells of *Posidonia australis* causing lysis of the thick polysaccharide material in the walls of the exodermal cells (Kuo et al., 1981). A suberin lamella restricts penetration, but fungi and bacteria occur in the lumen of exodermal and outer cortical cells. By analogy with terrestrial plants, it was suggested that rhizosphere organisms may be involved in nutrient uptake and nitrogen fixation in seagrasses. On the other hand, Nielsen et al. (1999) concluded that vesicular-arbuscular mycorrhizae cannot colonize the roots of *Zostera marina* and *Thalassia testudinum*, probably due to the effect of low oxygen supply and high salinity in marine sediments.

B. Rhizome and Stem

1. Morphology of Rhizome and Stem

Seagrass rhizomes are usually herbaceous, cylindrical to laterally compressed, and monopodially or irregularly branched; however, in *Amphibolis* and *Thalassodendron* (Fig. 1I), the rhizome branches sympodially and becomes woody. Rhizomes are almost always buried in sediment (the exceptions being *Thalassodendron* spp. and *Phyllospadix* spp.) and the persistent, fibrous remains of old leaf sheaths usually cover the rhizome of *Enhalus* and *Posidonia* (Fig. 1A and E), and to some extent *Zostera, Heterozostera, Phyllospadix* and *Halodule*. The lengths of rhizome internodes are relatively long in most of the genera, but they are extremely short in *Phyllospadix* (Barnabas, 1994b). Erect stems resulting from sympodial branching of rhizomes are present in all genera in the Cymodoceaceae (Fig. 1F–I), some species of *Heterozostera* (*H. nigricaulis* and *H. chilensis*) in the Zosteraceae, and *Thalassia* and some species of *Halophila* (Fig. 1B), in the Hydrocharitaceae. Erect stems form at each rhizome node in most genera, but only form at certain rhizome nodes in *Amphibolis, Thalassodendron* (Fig. 1I), *Thalassia* and *Heterozostera*. Among the above-mentioned genera, only *Amphibolis* has many branched stems, the others have few branches. Erect stems have numerous nodes representing leaf scars and can last for many years. In the genus *Halophila*, sections *Microhalophila, Spinulosae, Americanae* (Fig. 1B) and *Tricostatae*, all have distinct elongated stems but section *Halophila* (Fig. 1C) has very short erect stems. Erect stems of *Cymodocea, Halodule, Thalassodendron, Amphibolis, Heterozostera, Thalassia* and section *Spinulosae* of *Halophila* are rigid; while those of *Syringodium* and most of the *Halophila* species are soft and hegceous.

2. Anatomy of Rhizome and Stem

The internodes of rhizomes and erect stems are similar in transverse section, and have a similar tissue arrangement as those in roots. The epidermis is normally distinct and covered by a cuticle, and may contain tannin cells (Fig. 4C). Walls of epidermal cells are usually thickened and lignified. The exodermis is distinct and usually has more than one layer of cells with a thickened wall and a suberized middle lamella (Fig. 5A and B) (e.g. *Posidonia* and *Halophila*). Cortical parenchyma cells are larger in the outer region than in the inner one. Sometimes these two regions are very distinct, for example, in *Amphibolis* and *Thalassodendron*. Cells of the outer cortical parenchyma have thick, lignified walls, while those of the inner cortical parenchyma have thin, non-lignified walls. In this cortical tissue, large lacunae may develop, as in *Enhalus, Syringodium, Cymodocea* (Fig. 4C, D and H) *Zostera* and *Halophila* and the number of lacunae appears to be constant within genera. Unlike root tissues, beside the central stele, there are always two or more vascular bundles and numerous fiber bundles scattered among the outer cortical tissues in the rhizome and the erect stem (Fig. 4A–D). In addition, starch accumulates in the cortical parenchyma cells in some genera, e.g. *Enhalus* (Fig. 4G), *Thalassia, Zostera* and *Halodule*, but not in others (*Amphibolis* and *Thalassodendron*).

A conspicuous endodermis encloses the central stele and may become suberized (e.g. *Posidonia, Halodule*) or develop thickened and lignified walls (e.g. *Amphibolis, Thalassodendron*). The central stele has one or more central protoxylem elements surrounded by sieve tubes, but the pericycle is not distinct.

Underground rhizomes are a common feature of many monocotyledons and account for distinctive ecological features (Harper, 1977). The main functions of the rhizome in seagrasses are for anchoring, mechanical support, nutrient storage, and regulation and maintenance of vegetative growth. Tomlinson (1974) considered that vegetative propagation of rhizomes is probably of greater importance in the maintenance and spread of seagrasses than seed production.

The rhizomes of the larger species may, together with roots and leaf sheath remains, form dense mats. The seagrass *Posidonia oceanica* in the Mediterranean Sea usually grows on the thick ‘matte’ with a thickness of up to 4 m locally, constituting

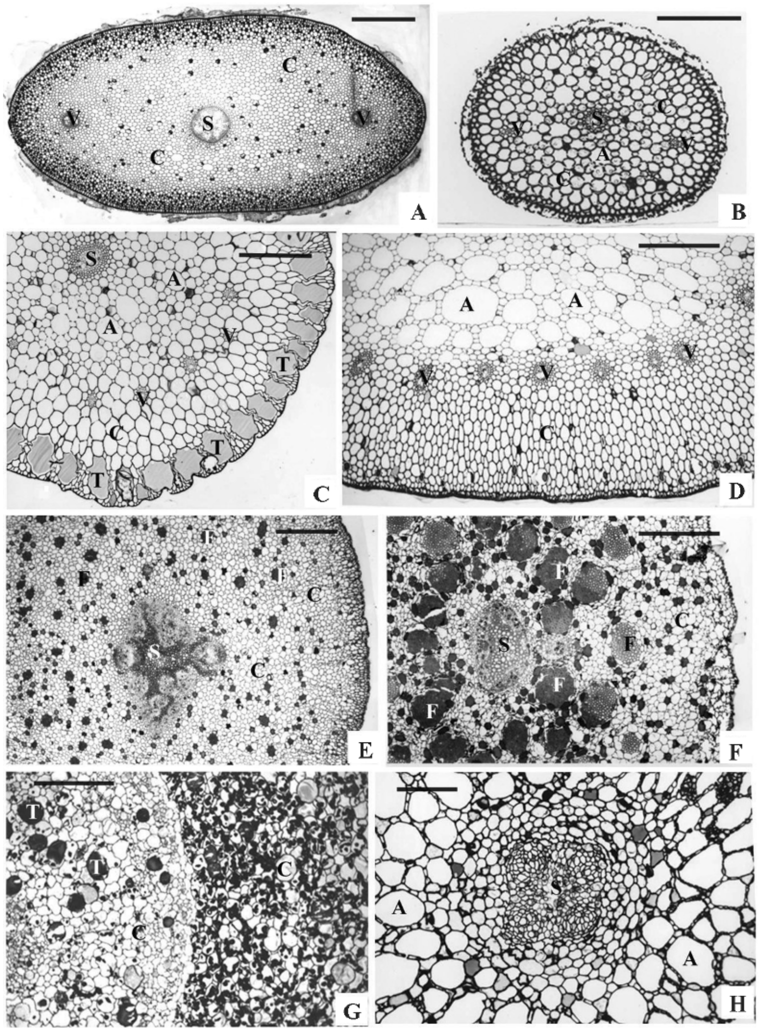

Fig. 4. Anatomy of rhizome and stem internodes. A. *Zostera caulescens*. Rhizome internode has a central stele (S), two opposite cortical vascular bundles (V) and a rather uniform cortical tissue (C). Scale = 700 μm. B. *Halodule uninervis*. Rhizome internode has a central stele (S), two opposite cortical vascular bundles (V) and a rather uniform cortical tissue (C). Scale = 200 μm. C. *Syringodium isoetifolium*. Rhizome internode has very distinct large tannin-containing cells (T) near the surface, and a ring of cortical vascular bundles (V) between the outer and inner cortical tissue (C). A few small air lacunae (A) occur near the stele (S). Scale = 100 μm. D. *Cymodocea nodosa*. Rhizome internode also has a ring of cortical vascular bundles (V), the compacted outer cortical tissue (C) and large air lacunae (A) occurring in the inner cortical tissue. Scale = 500 μm. E. *Posidonia australis.* Rhizome internode has numerous fiber bundles (F) scattering among the cortical tissue (C) almost reaching the centre stele (S). Scale = 100 μm. F. *Posidonia sinuosa.* Rhizome internode has smaller fiber bundles scattered in the cortex (C) and larger bundles (F) are restricted to the inner cortex and near the central stele (S). Scale = 500 μm. G. *Enhalus acoroides.* Rhizome internode has an outer cortex (C) rich in starch and an inner cortex (C) also having smaller starch grains and a few tannin cells (T). Scale = 500 μm. H. *Cymodocea nodosa.* Stem internode has a central stele (S) containing four distinct vascular poles and large air lacunae (A) occurring in the cortical tissue. Scale = 200 μm.

dead or living rhizomes, leaf sheath remains together with the sediment, which fills the interstices (see Fig. 13, Mateo et al., Chapter 7). Thus, rhizomes of this species grow in a horizontal (plagiotropic rhizomes) and a vertical (orthotropic rhizomes) plane (see Pergent, 1990). These leaf sheath remains in the matte can persist for more than 4600 years and show cyclic variation depending on environmental conditions such as light, temperature or water movement (Pergent, 1990; Di Dato, 2000) (see also Mateo et al., Chapter 7 and Gobert et al., Chapter 17). On the other hand, none of the Australian *Posidonia* species appears to be growing in a similar condition, although

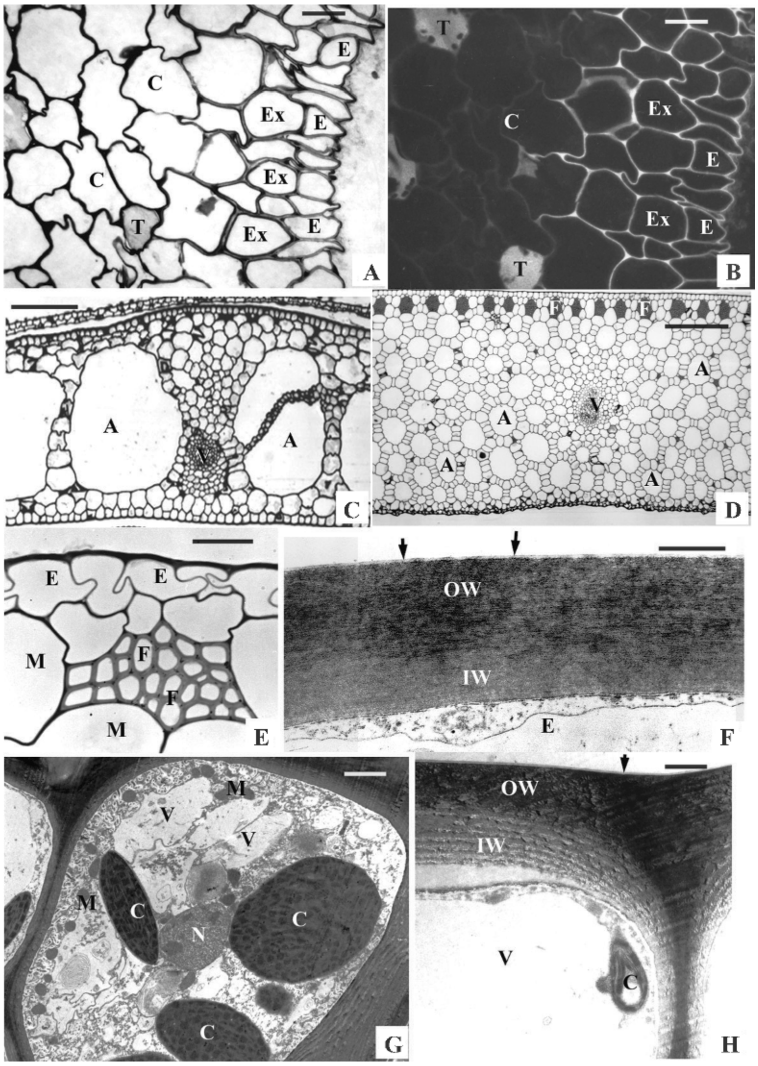

Fig. 5. Anatomy of rhizome internodes (A, B) and sheaths (C–H). A, B. *Posidonia australis*. Walls of the rhizome epidermal (E) and exodermal (Ex) cells are lignified and autofluorescent, a few tannin cells (T) occur in the cortical tissue (C). Scales = 50 μm. C. *Zostera marina*. Several large air lacunae (A) occur between two sheath longitudinal vascular bundles (V). Scale = 250 μm. D. *Posidonia kirkmanii*. Numerous smaller lacunae (A) occurring in the entire mesophyll tissues even near the longitudinal vascular bundle (V). Note that large fiber bundles (F) occur near the adaxial epidermal cells. Scale = 400 μm. E. *Posidonia australis*. Fibre cells (F) occur in the mesophyll tissue (M) near the adaxial epidermal cells (E) and walls of fiber cells are lignified. Scale = 50 μm. F. *Posidonia australis*. A thin, uniform electron transparent cuticle (arrows) and the outer tangential wall of the epidermal cell (E) has outer (OW) and inner (IW) regions. Scale = 1 μm. G. *Phyllospadix scouleri*. The adaxial sheath epidermal cell contains a nucleus (N), several chloroplasts (C), mitochondria (M), vacuoles (V) and wall ingrowths. Scale = 2 μm. H. *Phyllospadix scouleri*. The abaxial sheath epidermal cell contains a large central vacuole (V) and a few small plastids (C). The cuticle appears as a thin electron transparent layer (arrow), and the wall has outer wall (OW) and inner wall (IW) regions. Scale = 1 μm.

there is plenty of 'marine fiber' from leaf sheath remains deposited on the ocean floor. However, Davies (1970, Fig. 12) illustrated a tidal channel on the Wooramel Bank on the eastern margins of Shark Bay about 3 m deep cutting through *Posidonia* rhizome mesh (termed rhizome and root mesh) and deposits under living seagrass reached a maximum thickness of more than 7 m. The rhizomes of *Thalassodendron ciliatum* appear also to be very persistent forming extensive mats. As the decomposition of the material is very slow, these mats can attain a considerable thickness. Lipkin (1988) found living rhizomes up to 25 cm down in the mat, although it was very difficult to distinguish the old dark living rhizomes from dead material. In the Banda Sea, the mats were up to ca. 70 cm thick, and living rhizomes were only found in the upper 10 cm (Brouns, 1985). Further studies on the structure of the underground rhizome-root systems of the various seagrass species are recommended.

C. The Foliage Leaf

The foliage leaf is produced either from the rhizome nodes, normally from the upper side in *Enhalus, Halophila, Posidonia* and the Zosteraceae or from the apex of erect stems in *Thalassia* and the Cymodoceaceae. The foliage usually forms a unit of several leaves, and normally is referred to as a shoot containing different developmental stages. Each leaf consists of a basal leaf sheath and a distal leaf blade.

1. Leaf Sheath Morphology and Anatomy

The leaf sheaths are clearly differentiated from leaf blades, and enclose the young, developing leaves in all seagrass genera, which have strapped leaves. The leaf sheaths are usually covered by sediment at least at the base. Old ribbon leaf blades usually abscise at the junction between blade and sheath where there is a mechanical weakness in the structure of the epidermis and the structure and distribution of fiber cells (Tomlinson, 1972; Kuo, 1978), with the exception of *Amphibolis* and *Thalassodendron* where the leaf is shed in its totality, blade and sheath remaining together (den Hartog, 1970). A tongue-like structure known as the ligule is produced as an adaxial outgrowth at the junction of sheath and blade in all seagrasses except those in the Hydrocharitaceae. *Zostera* subgenus *Zostera* in the Zosteraceae has a tubular leaf sheath, which becomes ruptured with age. Leaf sheaths in all other genera are normally 'open,' i.e. split vertically, with opposite margins overlapping. The degree of this opening can sometimes be a useful diagnostic feature.

The general anatomy of the leaf sheath is similar to that of the blade, but detailed ultrastructures show marked differences (Fig. 5C and D). Furthermore, the structure of the outer and inner epidermis is significantly different (Fig. 5G and H). In contrast to the blade, the cuticle of the sheath epidermis appears as a thin, uniform, electron dense layer that is nonporous (*Posidonia*) (Kuo, 1978) (Fig. 5F) or lacks subcuticular cavities (*Zostera, Heterozostera, Phyllospadix*) (Kuo and Stewart, 1995) (Fig. 5H). The epidermis of the sheath lacks cell wall ingrowths, but has a large central vacuole with a thin peripheral cytoplasm, and chloroplasts, if present, occur only sparsely in the outer epidermal cells. The vascular bundles of the leaf sheath are similar to those in the blade, but there are no wall ingrowths in the vascular sheath cells and phloem parenchyma cells (in *Zostera* and *Heterozostera*), suggesting that in the leaf sheath there is little exchange of metabolites between the mesophyll and vascular tissue. Air lacunae and fiber bundles are more pronounced in the sheath than those in the blade (Fig. 5C and D). The fiber bundles of the sheath in *Posidonia* are lignified (Fig. 5E) and remain on the rhizome surfaces long after tissues of the leaf sheath have rotted away (Kuo, 1978).

Leaf litter from *Posidonia australis* and other species may accumulate on beaches, as high as 2 m along some parts of southern Australian coastline during the winter and, often, it is washed back into the ocean by late spring. In other locations, permanent deposits of up to 3 m in thickness occur. There is no doubt that these accumulations play an important role in marine food chains. Furthermore, the finally detached sheath fibers of *Posidonia* are rolled by wave action to form 'marine balls' or '*Posidonia* balls' of different sizes. Fiber balls have been recorded from Mediterranean beaches since ancient times, and are commonly observed along southern Australian coastlines. *Posidonia* fibers have accumulated on the ocean floor in such quantities in Spencer and Gulf St. Vincent in South Australia, that they were harvested for a time (1905–1915) to make grain bags, paper and insulation material (Winterbottom, 1917; Ried and Smith, 1919).

In contrast to the leaf blade in seagrasses, the leaf sheath probably has little function in the performance of photosynthesis or ion exchange with the surrounding media, but is very important in protecting the apical meristem and developing leaves. Tyerman (1989) showed that within the solution enclosed by the sheath, there is an osmotic gradient, created and maintained by ion uptake from the sheath.

2. Leaf Blade Morphology

In contrast to terrestrial monocotyledons, the surface of seagrass leaf blades is simple and naked (Fig. 6A–C and E–G) and only unicellular hairs occur on the surface of epidermal cells in certain species of *Halophila*, e.g. *H. decipiens* (Fig. 6D), *H. stipulacea* and *H. capricorni*. These hairs are

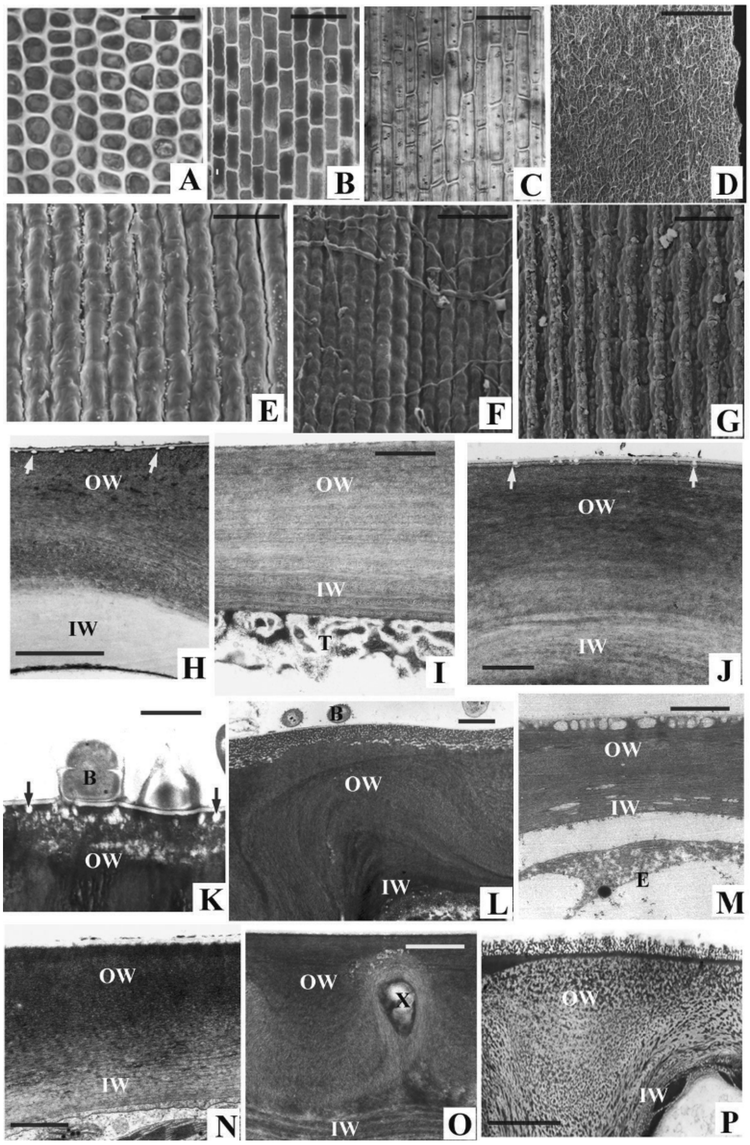

Fig. 6. Blade epidermal cells. A–C. Different *Posidonia* species have different appearance of the blade epidermal cells. A. *Posidonia australis*, B. *P. sinuosa*, C. *P. angustifolia*. Scales, all = 20 μm. D. *Halophila decipiens*. Numerous hairs occur on the surface and uneven blade margins. Scale = 500 μm. E–G. Different *Phyllospadix* species have different appearance of the blade epidermal cells. E. *Phyllospadix scouleri*, F. *P. torreyi*, G. *P. japonica*. Scales E = 20 μm, F = 50 μm, G= 20 μm. H. *Enhalus acoroides*. A cuticle with small subcuticular cavities (arrows). The walls have two distinct regions: an outer (OW) more electron dense and an inner (IW) electron transparent region. Scale = 1 μm. I. *Halophila ovalis*. An electron transparent cuticle covers cell walls, which possess an outer (OW) and the inner (IW) region. Note that wall ingrowths (T) on the inner face of the walls. Scale = 1 μm. J. *Zostera muelleri*. A cuticle with small subcuticular cavities (arrows), the wall also consists of outer (OW) and inner (IW) regions. Scale = 1 μm. K. *Phyllospadix iwatensis*. The cuticle has small subcuticular cavities (arrows). Bacteria (B) may have altered the compositions of the outer wall region (OW). Scale = 0.5 μm. L. *Posidonia australis*. Some bacteria are associated with the porous cuticle. The cuticle covers outer wall (OW) and inner wall (IW) regions. Scale = 1 μm. M. *Cymodocea angustata*. A cuticle with numerous large subcuticular cavities (arrows), the wall has both the outer (OW) and the inner wall (IW) regions, and covering the epidermal cell (E). Scale = 1 μm. N. *Syringodium isoetifolium*. A thin electron transparent cuticle covers the outer (OW) and inner (IW) wall region. Scale = 1 μm. O. *Thalassodendron pachyrhizum*. A thin electron transparent cuticle with complex inclusions in the outer wall (OW) and lamellae arrangements in the inner wall (IW) region. Scale = 1 μm. P. *Amphibolis antarctica*. An electron dense layer lies between the porous cuticle and the outer heterogenous wall (OW) and the lamellae inner wall (IW) region. Scale = 1 μm.

usually more pronounced on the abaxial than the adaxial surface. Unicellular short hairs/spines or ‘marginal teeth’ often occur in the leaf blade margins (Fig. 6D); in particular, toward the leaf apex as in *Cymodocea, Thalassodendron, Phyllospadix* (‘fin cells’), *Thalassia* and most species of *Halophila*. These features are often taken to be taxonomically diagnostic.

The shape of epidermal cells in surface view may differ between seagrass species, and has been used as a species identification character in certain genera; e.g. in *Posidonia* (Fig. 6A–C), *Phyllospadix* (Fig. 6E–G), *Heterozostera* and *Halophila* (Kuo, 1978; Kuo and McComb, 1989; Kuo et al., 1988; Kuo and Stewart, 1995; Cambridge and Lambers, 1998; Kuo, 2005). The appearance of the leaf apex has also been used as an important diagnostic feature for identifying certain seagrass genera including *Zostera, Halodule* and *Amphibolis* (den Hartog, 1970). However, the reliability of this feature has been questioned for identifying species of *Halodule* (Phillips and Meñez, 1988).

3. Leaf Blade Anatomy and Ultrastructure

Anatomically, the arrangement of tissues and cells in the adaxial and the abaxial sides of a strap leaf blade is identical, but the position of xylem elements (adaxial side) in the vascular bundles can usually be used to determine which side is which (Fig. 8A and B).

The most obvious differences in anatomical structure of seagrasses from those of terrestrial plants are: (a) a lack of stomata (Fig. 6A–G); (b) extremely thin cuticle (Fig. 6H–P); (c) epidermis acting as the major photosynthetic site; and (d) reduced water conducting elements. Otherwise, other cell types and tissues may be similar or slightly different among different seagrass groups. The leaf blade anatomy of seagrasses does not correspond to either the typical C_3 or C_4 anatomy of terrestrial plants.

a. Leaf Cuticle

Ultrastructurally, there are three distinct types of cuticle in seagrasses and they appear to be genus specific. (a) The cuticle appears as a thin, uniform electron transparent layer, 0.1–0.2 μm thick, as in the case of *Halophila, Thalassodendron* and *Syringodium* (Fig. 6I, N and O). (b) It may appear as a thin, electron transparent layer, 0.05 μm thick, with ‘subcuticular cavities’ at or near the junction between the cuticle and the outer most tangential cell walls as in *Enhalus, Zostera, Heterozostera, Phyllospadix* and *Cymodocea* (Fig. 6H, J, K and M). (c) The cuticle appears porous in texture and 0.5 μm thick, as in the case of *Thalassia, Posidonia* and *Amphibolis* (Fig. 6L and P). Despite marked differences in their appearance, the functions of the cuticle may be very similar (see below).

b. Leaf Epidermis

Epidermal cells are normally small, about 10–30 μm in diameter. Histochemically and ultrastructurally, the walls are different. The thicker outer tangential walls mainly consist of polysaccharides and protein with little cellulose, and are never lignified. They appear as two distinct zones: the outer one is more packed with microfibers and the inner one has a lamellar appearance (Fig. 6H–P). Whether there is any functional difference in these two zones has yet to be established. The radial wall is tapering from the outer walls toward the inner ones and mainly consists of cellulose. The inner tangential walls have a uniform lamellar appearance and wall ingrowths may occur in certain species (Fig. 6I; see below).

A distinctive feature of the epidermis of certain seagrasses is the presence of wall ingrowths, a characteristic of transfer cells in many terrestrial plants associated with a convoluted plasmalemma with a relatively large surface area (Gunning and Pate, 1968; Gunning, 1972; Pate and Gunning, 1972) (Figs. 6I and 7A, C and E). This peculiar structure was speculated to have an association with osmoregulation and nutrient uptake in seagrasses (Jagels, 1973; Doohan and Newcomb, 1976). However, such structures are normally more pronounced on the inner than the outer tangential wall, even though they are absent in certain genera e.g. *Posidonia* (Fig. 7D), *Amphibolis* and *Syringodium* (Fig. 7G). These facts suggest that the epidermal wall ingrowths, reminiscent of transfer cells may not be associated with nutrient uptake and osmoregulation in seagrasses. Furthermore, it has been reported that plasmodesmata are present at earlier stages of leaf development, but disappear in the mature leaf epidermis of *Z. marina* and *T. testudinum* (Jagels, 1983). These observations indicate that there appears to be no cytoplasmic continuity (plasmodesmata) between the epidermal and underlying mesophyll cells in those species possessing wall ingrowths. This implies

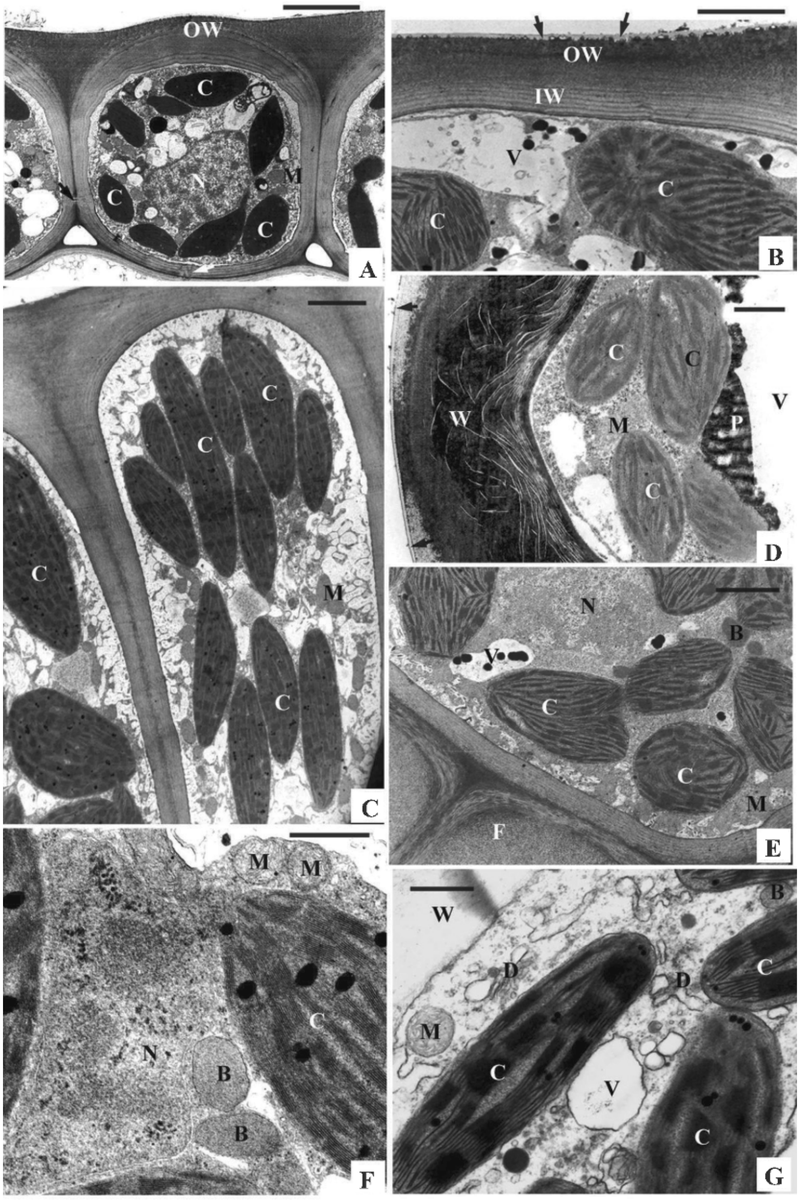

Fig. 7. Blade epidermal cells. A. *Enhalus acoroides*. Plasmodesmata (arrows) occur between two epidermal cells and between the epidermal and the mesophyll cells. Wall ingrowths occur mainly in the radial and the inner tangential cell walls. The cell also has a nucleus (N), and several chloroplasts (C). Scale = 4 µm. B. *Thalassia hemprichii*. The cuticle has subcuticular cavities (arrows), and the wall (W) has outer (OW) and inner wall (IW) regions. The cell contains large chloroplasts (C) and vacuoles (V) with electron dense substances. Scale = 2 µm. C. *Phyllospadix torreyi*. Cells with numerous chloroplasts (C) and mitochondria (M). Note very fine wall ingrowths occur in the inner wall faces. Scale = 2 µm. D. *Posidonia sinuosa*. The cuticle appears as a thin electron transparent layer, while the wall has an unusual lamellate appearance. The cell contains chloroplasts (C), mitochondria (M) and a central large vacuole (V) with polyphenolic substance (P). Scale = 1 µm. E. *Thalassia hemprichii*. The cell contain a nucleus (N), chloroplasts (C), mitochondria (M) and vacuoles (V) with electron dense substances. Wall ingrowths occur mainly in the radial and inner tangential walls even those adjacent to fiber cells (F). Scale = 2 µm. F. *Heterozostera nigricaulis*. The cells have a nucleus (N), mitochondria (M) and chloroplasts (C) with electron dense lipids. Note microbodies (B) are also present. Scale = 2 µm. G. *Syringodium isoetifolium*. Cells have chloroplasts (C), mitochondria (M), vacuoles (V) and dictyosomes (D). Scale = 1 µm.

that nutrient movement is apoplastic in these seagrasses (see Kuo and McComb, 1989). On the other hand, a well-developed system of plasmodesmata connects adjacent epidermal and mesophyll cells in *Enhalus* (Fig. 7A), *Posidonia* spp., and also in *Zostera muelleri* and *Phyllospadix* spp. suggesting that symplastic communication in these species is possible (see Kuo and McComb, 1989; Kuo and Stewart, 1995).

The epidermis of the leaf blade is the major site of photosynthesis for seagrasses and some fresh water plants, in contrast to terrestrial plants (see also Larkum et al., Chapter 14). In all species of seagrasses, the epidermis has high concentrations of chloroplasts, contains mitochondria, lipid droplets, dictyosomes, endoplasmic reticulum and microbodies; small starch grains are present in *Thalassodendron* and *Amphibolis*. The vacuoles of *Enhalus* (Fig. 7A), *Thalassia* (Fig. 7B and E), *Posidonia* (Fig. 7D), *Halodule, Cymodocea, Amphibolis* and *Thalassodendron* contain a polyphenolic substance (tannin) but those of *Zostera, Heterozostera* and *Phyllospadix* (Fig. 7C and F) do not have tannin.

Various cytoplasmic components, including paramural bodies, endoplasmic reticulum, dictyosomes and microtubules were observed during the initiation and subsequent development of wall ingrowths in the epidermis of *Zostera* leaves (Barnabas et al., 1982; Jagels, 1983). However, the precise relationship between the presence of these organelles and the synthesis of wall ingrowths remains uncertain (see Kuo and McComb, 1989).

c. Leaf Fiber Cells

The occurrence of prominent fiber cells in the leaf blade is of particular interest (Fig. 8B–E). They are present as strands of various sizes in the leaves of certain genera but absent from others. The distribution and the size of these fiber strands may even differ among species within a genus, e.g. in *Zostera* and *Posidonia* and can be used as species identification characters. Fiber strands are normally abundant near the leaf margins, associated with longitudinal vascular bundles and also present in the hypodermis adjacent to air lacunae (Fig. 8C and D). A fiber strand usually consists of several fiber cells with thickened but not lignified walls (Fig. 8D and E). Thus, together with the thick walled epidermal cells, they could provide tensile strength but retain a degree of flexibility, allowing the strap-shaped leaf blades to withstand vigorous wave action. In *Posidonia*, fiber strands are present in the hypodermal and subhypodermal layers of those species having flattened blades, but also occur deep in the mesophyll in species with biconvex to terete blades. In contrast, in the family Cymodoceaceae, fiber strands are only present in *Cymodocea* and are absent from the remaining four genera (Fig. 8I–K). Despite the fact that *Thalassodendron* and *Amphibolis* often grow in high-energy environments, their leaves are usually carried on the tips of long, flexible stems and their blades are extremely thin but strengthened with thick-walled bundle sheath cells that compensate for the absence of fiber strands. In contrast, both *Halodule* and *Syringodium* have enlarged aerenchyma systems and normally inhabit sheltered areas. Fibrous strands are also reduced in leaf blades of *Halophila, Ruppia* and *Lepilaena*, but all these genera have thin leaf blades with few mesophyll cells and few air lacunae.

d. Leaf Mesophyll and Air Lacunae

The mesophyll tissue of seagrasses is homogeneous with thin-walled but highly vacuolated parenchyma cells (Figs. 8A and B and 9A–C). The thin peripheral cytoplasm contains few chloroplasts with small starch grains. The mesophyll cells surround air lacunae of varying size; in some genera there are prominent and regularly arranged (about 3–5) air lacunae separating longitudinal vascular bundles, e.g. in *Heterozostera, Phyllospadix Zostera* (Figs. 8A and 9A and B), *Thalassia* and *Enhalus*. Air lacunae are present in *Posidonia* (Figs. 8B and 9C), but less prominent than in the above genera. In the leaves of *Halophila, Amphibolis* and *Thalassodendron* lacunae are present though minute in size (Fig. 8I and J). It is generally assumed that aerenchyma is developed to increase the internal gas space of aquatic plants as they may grow in oxygen poor substrata (see also Borum et al., Chapter 10).

Air lacunae are interconnected in all vegetative and reproductive organs of all seagrass species, i.e. leaves, petioles, rhizomes, stems, roots and flowers and fruits). They are interrupted by septa between organs and also at regular intervals in particular organs, e.g. leaves by perforated septa (Fig. 9E–G). Each septum consists of a group of small parenchyma

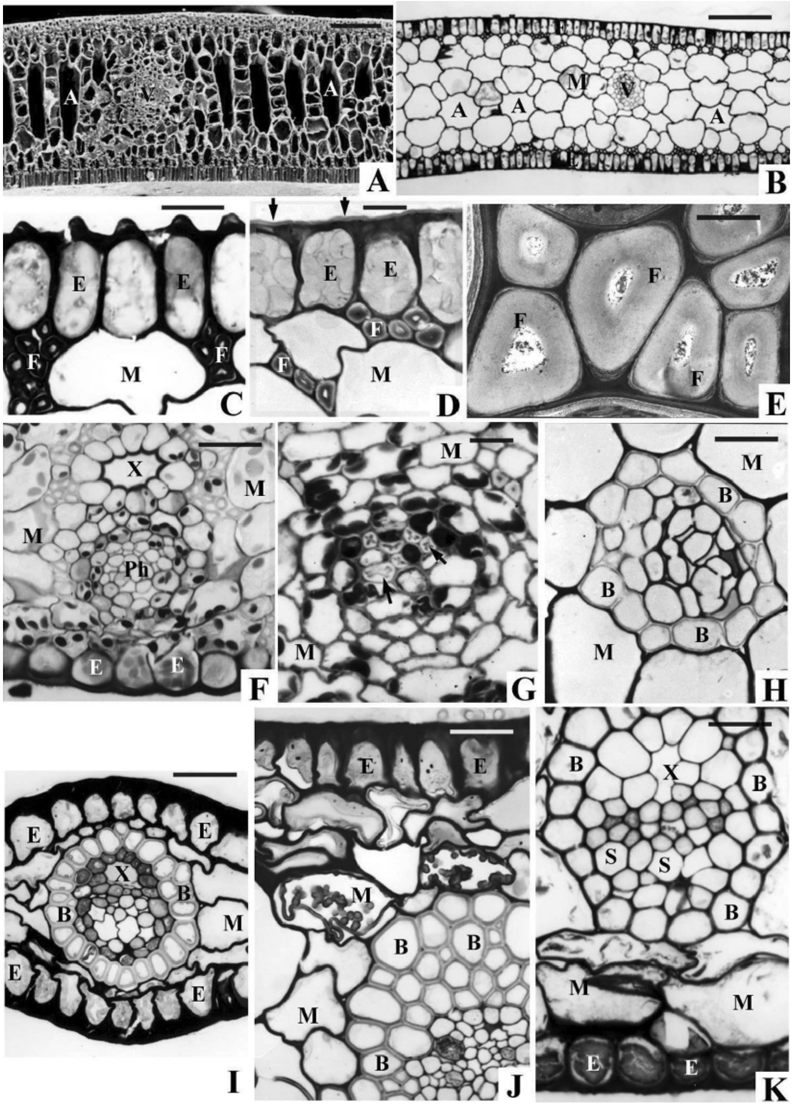

Fig. 8. Anatomy of leaf blades. A. *Phyllospadix iwatensis*. The blade has a similar tissue arrangement between the abaxial and adaxial surfaces with a vascular bundle (V) and distinct air lacunae (A) in the centre. Scale = 100 μm. B. *Posidonia australis*. The abaxial and the adaxial sides of the blade are identical with a vascular bundle (V) in the centre, but air lacunae (A) are not so distinct. Scale = 200 μm. C. *Phyllospadix japonica*. Each epidermal cell (E) has an outer protrusion and group of fiber cells (F) occur between the epidermal cells and the mesophyll tissues (M). Scale = 15 μm. D, E. *Posidonia australis*. A distinct cuticle (arrows) is present in the epidermal cells (E), fiber cells (F) abut the epidermal cells and the mesophyll tissue (M). Each fiber cell (F) has thick and uniform electron dense walls with a small lumen. Scales D = 10 μm, E = 5 μm. F and G. *Zostera muelleri*. The xylem (X) is separated from the phloem tissue (Ph), which has several nacreous wall sieve tubes (arrows). M = mesophyll cells. Scales: F = 30 μm, G = 10 μm. H. *Posidonia australis*. Walls of bundle sheath cells (B) are lignified. Scale = 20 μm. I. *Thalassodendron pachyrhizum*. Walls of bundle sheath cells (B) are thickened and lignified. E = epidermal cells and M = mesophyll cells. Scale = 50 μm. J. *Amphibolis antarctica*. There are two to three layers of bundle sheath cells (B). Walls of these cells are thickened and lignified. Note that small starch grains occur as black dots in the epidermal cells (E), and few mesophyll cells (M) contain tannins. Scale = 40 μm. K. *Halodule uninervis*. Bundle sheath cells (B) have no special feature. The phloem has both normal sieve tubes (S) and nacreous wall sieve tubes, and xylem vessel has a large lumen (X). Scale = 25 μm.

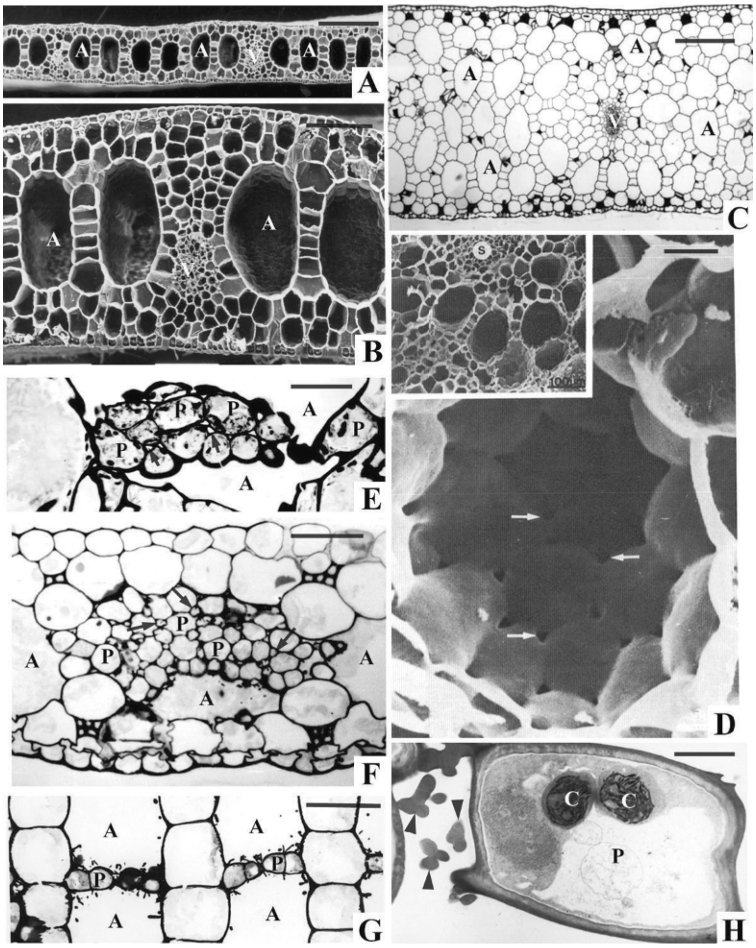

Fig. 9. Anatomy of aerenchyma. A, B. *Zostera marina*. Five or six large air lacunae (A) are present between two longitudinal vascular bundles (V). Scales A = 300 µm, B = 100 µm. C. *Posidonia australis*. Numerous smaller aerenchyma lacunae (A) are scattered among the mesophyll tissue. Scale = 350 µm. D. *Halophila ovalis*. Intercellular pores (arrows) in the lacunal diaphragm at the rhizome node (after Roberts et al., 1984). Scale = 5 µm. E. *Halodule uninervis*. Intercellular pores (arrows) in the leaf blade lacunal septum. Scale = 40 µm. F–H. *Zostera muelleri*. Wall protrusions (arrowheads) of septal parenchyma cells (P) project into intercellular pores (arrows) of the lacunal septa in the leaf blade air lacunae (A). Scales F = 20 µm, G = 50 µm, H = 3 µm.

cells with minute intercellular spaces (pores) (Fig. 9E and F), these are about 0.5–1.0 µm in diameter in *H. ovalis* (Fig. 9D) (Roberts et al., 1984). The pores are sufficiently large to permit movement of gas molecules, but are too small to permit the movement of a gas-water interphase bubble. In addition, numerous wall protuberances, ca. 1 µm in diameter, project into these spaces (pores) in *Z. muelleri* and *Z. capricorni* (Fig. 9F–H). These pores and wall protuberances may function as 'internal stomata' to regulate the gas flow within the aerenchyma (Larkum et al., 1989). The septa can act to prevent the collapse of the aerenchyma system, provide a physical barrier to flooding but allow gas continuity to be maintained within the lacunar system, and provide lateral gas transport across the cortex into roots, rhizomes and stems or the parenchymatous mesophyll in blades and sheaths, i.e. from the rhizosphere to the stele in roots, rhizomes and stems and from the phyllosphere to the vascular systems (and *vice versa*). Furthermore, air lacunae are considered important in seagrass photosynthesis (Roberts and Moriarty, 1987). It has been shown that air lacunae contain nitrogen, oxygen and carbon dioxide (see Borum et al., Chapter 10) and Zelich (1971) estimated that 50–67% of photorespired carbon dioxide in *T. testudinum* leaves is recycled.

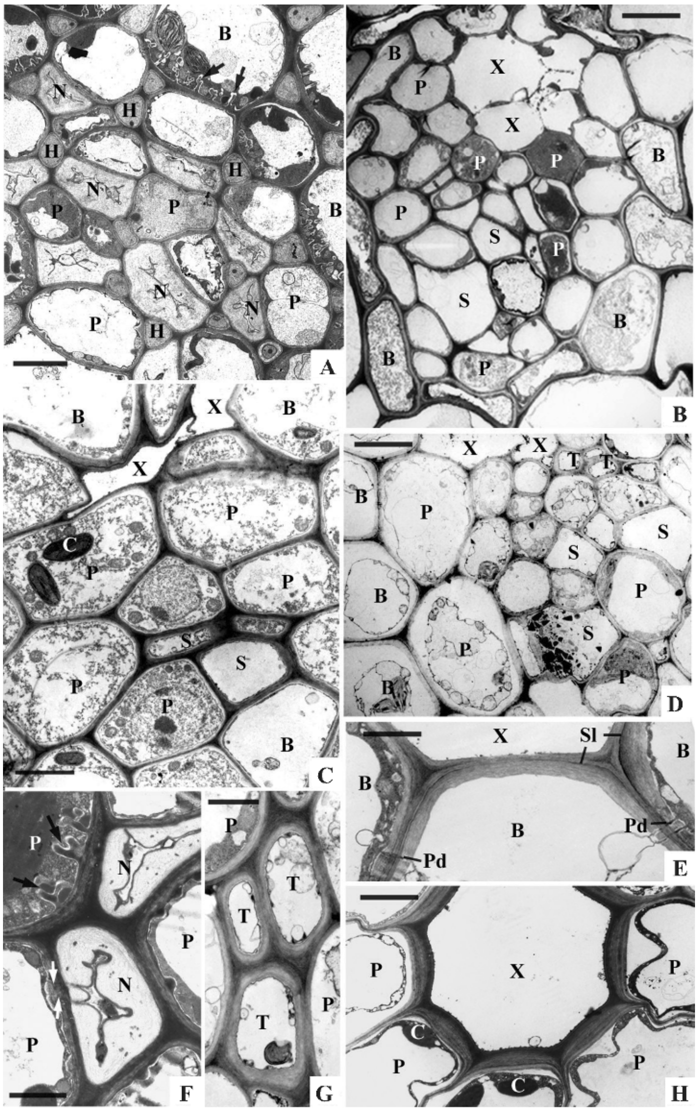

Fig. 10. Vascular tissues. A. *Zostera muelleri* (subtidal form). Wall ingrowths (arrows) occur on the inner tangential walls of the vascular bundle sheath cells (B). Nacreous wall sieve tubes (N) are associated with vascular parenchyma cells (P), note a few fungal hyphae (H) occur in the intercellular spaces. Scale = 5 μm. B. *Posidonia australis*. Cell walls of the vascular bundle sheath cells (B) are lignified. Sieve tubes (S) and parenchyma cells (P) are normal, xylem vessels (X) have little secondary wall thickening. Scale = 5 μm. C. *Cymodocea serrulata*. Vascular bundle sheath cells (B), sieve tubes (S), parenchyma cells (P) and xylem vessels (X) are normal and do not have special modifications. Scale = 4 μm. D, E. and G. *Syringodium isoetifolium*. Walls of the vascular bundle sheath cells (B) have suberized lamellae (Sl). The species has both normal sieve tubes (S) and thickened-wall sieve tubes (T) abutting xylem vessels (X). Scales D = 4 μm, E = 1 μm, G = 1 μm. F. *Phyllospadix iwatensis*. Nacreous wall sieve tubes (N) have uneven wall thickness and lumens, and also have plasmodesmata (white arrows) connecting vascular parenchyma cells (P), which posses wall ingrowths (black arrows). Scale = 5 μm. H. *Zostera muelleri*. Walls of xylem parenchyma cells (P) that abut xylem (X) are thickened. Scale = 5 μm.

e. Leaf Vascular System

The strapped-leaved blades of seagrasses always possess three or more parallel longitudinal veins, which are interconnected, by transverse veins at regular intervals. However, *Enhalus*, unlike other seagrasses, has several additional smaller lateral veins forming a separate adaxial and abaxial vascular system. Seagrasses without a strap-leaved blade, such as *Halophila*, have a midvein and two lateral 'intra-marginal veins,' which are joined at the base and top and are interconnected by several 'cross veins' in the blade. Vascular systems of seagrasses are similar in structure and composition to those of other vascular land plants, and all have sieve and xylem elements and vascular parenchyma cells (Fig. 8F–K). However, the so-called companion cells that are usually associated with sieve tubes in terrestrial plants are not distinct (Fig. 10A–D) and thus are referred to as vascular parenchyma cells in this chapter.

A distinct layer of sheath cells always encloses each longitudinal vascular bundle of the strap-shaped leaf and the structure of these sheath cells differs between genera: (a) sheath cells have thin and lignified walls in *Posidonia* (Figs. 8H and 10B); (b) sheath cells have thick, unlignified walls, but possess a suberized lamella in *Thalassodendron* and *Amphibolis* (Fig. 8I and J) (Barnabas and Kasvan, 1983; Kuo, 1983a); (c) sheath cells have thin and unlignified walls but possess a suberized lamella in *Syringodium* (Fig. 10D and E) (Kuo, 1993a); (d) sheath cells have wall ingrowths in the inner tangential walls in *Zostera* and *Heterozostera* (Fig. 10A) (Kuo, 1983a); and (e) sheath cells appear to have no obvious structural specialization in all other genera, e.g. *Halodule, Cymodocea* (Fig. 10C) and *Halophila* (Kuo, unpublished). Regardless of the difference in the structure, it has been speculated that bundle sheath cells in seagrasses, as with those in terrestrial plants, might be involved in restricting solute transfer between the mesophyll and the vascular tissue to a symplastic pathway (Kuo and McComb, 1989; Kuo, 1993a). This has been demonstrated by dye transpiration experiments in *Thalassodendron* and *Halodule* leaves (Barnabas, 1989, 1994a).

Sieve elements in seagrasses are of three anatomical types. (a) Elements that are thin-walled with a relatively large lumen; these occur in all seagrass genera (Fig. 10B–D). (b) Elements that are not lignified with an irregular wall thickening and an uneven inner surface; thus having varied lumen dimensions along the element. This type of sieve tube is known as a nacreous-walled sieve element and occurs only in the Zosteraceae (Figs. 8G and 10A and F) and in *Halodule* of the family Cymodoceaceae (Kuo, 1983b). (c) Elements that are small with evenly thick walls and a small lumen. This element always abuts with xylem and has only been recorded in *Syringodium* (Fig. 10D and G) (Kuo, 1993a) and *Thalassodendron* (Barnabas, 1983). Despite the difference in their locations and appearances, all three types of sieve elements have similar cytoplasmic properties, with a distinct plasmalemma and contain mitochondria, stacked smooth endoplasmic reticulum, typical monocotyledonous plastids with protein crystalloids, and lack a nucleus and ribosomes at maturity. In addition, there are many symplastic connections from sieve elements to adjacent vascular parenchyma cells via sieve areas along their common walls (Fig. 10G and F). These observations suggest that all three types of sieve elements are functional. However, the precise functions, such as the degree of effectiveness in solute translocation or temporary solute storage as suggested for terrestrial plants, have yet to be determined in the sieve elements of the marine angiosperms. Various types of sieve tube are not unique to seagrasses, as they have also been found in the vascular bundles of terrestrial plants.

Aquatic plants generally are characterized by reduced xylem tissue. This reduction is interpreted as a result of the loss of functional need (mechanical and conductive) in plants with a constant supply of water and supported by the aqueous medium (Sculthorpe, 1967). Vessels are essentially absent and the tracheary elements are mostly reduced in all submerged species. They may be represented by weakly lignified elements with annular or spiral wall thickening, and minimal amount of secondary wall material (Tomlinson, 1982). In the Zosteraceae, the xylem and phloem are totally separated (Fig. 8F) and the xylem is represented by a single wide lacuna surrounded by a distinct layer of large xylem parenchyma cells with thickened but not lignified walls, a feature that distinguishes them from other seagrasses (Fig. 10H). Ultrastructurally, the xylem wall of *Zostera* and *Phyllospadix* appears to be completely hydrolyzed and the so called ‘xylem wall’ in fact is represented only by the middle lamella, which appears as an electron dense layer, and the thickened wall of the adjacent xylem parenchyma cells (Fig. 10B). On the other hand, in other families, xylem and phloem are together and xylem elements have highly hydrolyzed walls with little, e.g. *Posidonia* (Fig. 10G), or no lignification, e.g. *Halophila, Cymodocea* (Fig. 10C) and *Syringodium* (Fig. 10E). The reduced xylem has led to a suggestion that there is little xylem transport in seagrasses (Tomlinson, 1982), and an experimental study on this topic is highly recommended.

The structure of the vascular parenchyma cells is very similar in all seagrasses, except for the Zosteraceae, in which wall ingrowths occur in phloem parenchyma cells. Vascular parenchyma cells (Fig. 10F) usually contain several chloroplasts (with poorly developed grana), mitochondria, lipid droplets, free ribosomes and rough endoplasmic reticulum, as well as plastids with electron-opaque bodies resembling protein crystalloids. Branched plasmodesmata with enlarged walls frequently form connections between vascular parenchyma cells.

f. Phyllosphere

Seagrasses often bear epiphytes including bacteria, diatoms, algae, hydroids and sponges (see Borowitzka et al., Chapter 19). Some filamentous bacteria have been also associated with decaying seagrass leaves by tunneling thick outer tangential and radial walls in *T. testudinum* (Porter et al., 1989) and in *T. ciliatum* (Barnabas, 1992). On the other hand, symbiotic fungal hyphae have been reported only from *Z. muelleri*, but only in its subtidal form. These fungal hyphae have been observed throughout the leaf intercellular spaces and might be involved in enhancing solute transfer within the seagrass leaf (Kuo, 1984; Kuo et al., 1990a).

Webster and Stone (1994b) concluded that the wall composition of vegetative parts of *Heterozostera nigricaulis* (as *H. tasmanica*) is quite unlike that of terrestrial graminaceous monocotyledons and is more akin to the walls of dicotyledons. Chemistry and biochemistry of wall compositions in other seagrass species are also discussed in detail by Mateo et al., Chapter 7.

IV. Reproductive Morphology and Anatomy

A. Flowers

1. Reproductive Strategies

Generative reproduction is carried out in seagrasses by regular flowering. The majority of seagrass species are perennial and only certain populations of *Zostera marina* (Keddy and Patriquin, 1978; McMillan, 1983b; Van Lent and Verschuure, 1994; den Hartog, unpublished), *Halophila decipiens* (McMillan and Soong, 1989; Kuo and Kirkman, 1995; Kenworthy, 2000), and *Halophila tricostata* (Kuo et al., 1993) have been identified as annuals. The perennial populations may show both generative and vegetative growth, while the annul populations depend completely on generative growth i.e. recruitment from seeds.

Nine of the 12 seagrass genera are dioecious (although some species of *Halophila*, e.g. *H. decipiens, H. capricorni* and *H. beccarii* are monoecious), in comparison with less than 10% of the entire number of angiosperm genera. Dioecy probably plays an important role in the outcrossing mechanism in seagrasses (McConchie and Knox, 1989a; see also Waycott et al., Chapter 2 and Ackerman, Chapter 4). The Posidoniaceae are exclusively monoecious; in contrast, the Cymodoceaceae are entirely dioecious, while the marine Hydrocharitaceae and the Zosteraceae contain both monoecious and dioecious genera. All genera of the eurysaline aquatic plants are monoecious, with the exception of *Lepilaena*, which has monoecious as well as dioecious taxa.

Most aquatic plants retain the floral systems of their terrestrial ancestors, which were not originally adapted to function in water. Some species have acquired floral modifications that allow pollination to function efficiently in aquatic habitats, a phenomenon known as hydrophily. For the reproductive organs, seagrasses exhibit unique structural adaptations for marine submerged pollination. Many floral structures in seagrasses are simplified with a reduced perianth in comparison with terrestrial flowering plants, and these structures may vary with seagrass groupings. This fact indicates that the affinities between the seagrass families are not at all clear (Tomlinson, 1982). Furthermore, it also reflects the fact that seagrasses have evolved from more than one common ancestor, through different evolutionary pathways, and geological periods (den Hartog, 1970; Larkum and den Hartog, 1989; Philbrick and Les, 1996; Les et al., 1997). Most of their freshwater or terrestrial cousins no longer exist and identification of seagrass evolutionary pathways is quite difficult, if not impossible (but see Chapters 1 & 2).

Floral development and morphology in seagrasses have been reported in several species including *Amphibolis* (see McConchie and Knox, 1989a). In *A. antarctica*, the flowers form on lateral branches while in *A. griffithii*, they may also develop terminally on an upright branch from the rhizome. Female flowers develop from a pair of primordia, which, in *A. griffithii* develops three stigmas, while in *A. antarctica*, may form secondary branches. The ovary wall bears the initials of the grappling apparatus, comprising four comb initials in *A. griffithii* and a further inner set of horns in *A. antarctica*.

2. Hydrocharitaceae

In the Hydrocharitaceae, dioecious *Enhalus* has a many-flowered male inflorescence on a short peduncle, enclosed by the leaf sheaths, usually referred to as a spathe. Each mature flower is thinly pedicellate, with six tepals and three stamens. At maturity they break free and float in dense patches on the surface. The female flower is solitary on a long peduncle and is enclosed by two overlapping bracts, extending and floating on the surface at maturity (Fig. 13A). Each female flower has three tepals, three recurved sepals, erect petals and six branched styles. The ovary is compressed, with several anatropous ovules. In dioecious *Thalassia*, the inflorescence is usually single; each has a separate spathe on short shoots. Each unit can be interpreted as a one-flower inflorescence.

Most *Halophila* species are dioecious, the exceptions being *H. decipiens, H. beccarii, H. capricorni* and *H.* sp. allied to *H. ovalis* from Indonesia (Kuo, unpublished), which are monoecious. However, the flower formation in the three monoecious *Halophila* species is different. Both male and female floral shoots of *H. decipiens* are produced at the same rhizome nodes (Kuo et al., 1995) (Fig. 11A), while either male or female floral shoots of *H. beccarii* (Parthasarathy et al., 1988, Muta Harah et al., 1999), *H. capricorni* (Larkum, 1995) and *Halophila* sp. being formed on separate rhizome nodes of the same plants (Fig. 13C). Regardless whether they are monoecious or dioecious, flowers of *Halophila* are unisexual, almost always solitary, and enclosed by two overlapping spathes (bracts) (Fig. 11B). In the species with erect stems, e.g. *H. tricostata, H. spinulosa, H. engelmanni*, etc., flowers are produced at each distal node of an erect stem and flowers and fruits mature acropetally along the erect shoot during the reproductive season (Kuo et al., 1993). For the species without erect stems, e.g. *H. ovalis, H. stipulacea, H. decipiens*, etc., flowers develop and mature progressively at each node along the rhizome branches. This results in the oldest fruits being furthest from the youngest shoot apex (Kuo and Kirkman, 1995). The male flower has three imbricate tepals, which enclose three anthers. At anthesis, the pedicel extends upwards and the tepals become distinctly swollen and bright yellow, sometimes with pigments (Figs. 11A and 12A), then the tepals open to release pollen from the anthers (Fig. 12B). The entire male flower detaches from the plant immediately after anthesis. The female flower consists of an ovary with three parietal placentae containing several to numerous ovules and a hypanthium extending into 2–6 filiform styles. After anthesis, styles detach, but the hypanthium persists (Fig. 13C).

3. Zosteraceae

In the Zosteraceae, the inflorescent shoots (known as generative shoots) initiate as terminal or lateral branches at rhizome nodes in all species in *Zostera* as well as two species in *Heterozostera* (*H. tasmanica* and *H. polychlamys*) (see Kuo, 2005). Thus, the mature reproductive shoot-bearing node usually appears a few rhizome nodes behind the vegetative shoot-bearing node of the extending rhizome. The mature generative shoot has repeated branching with a conspicuous basal membranous prophyll at each branch and bears one to three inflorescences on each branch. Each generative shoot is normally terminated with a generative branch in all *Zostera* and *Heterozostera* species except in *Z. caulescens* and *H. nigricaulis* and possibly *H. chilensis*. In *Z. caulescens*, the generative shoot is terminated with a sterile branch with several vegetative leaves, resulting in this species growing up to 7 m long (Aioi et al., 1997). *H. nigricaulis* and *H. chilensis* produce rigid black erect stems, which bear an inconspicuous spadix amongst a tuft of leaves at the top of *H. nigricaulis* (Kuo, 2005). *Phyllospadix torreyi* has a prolonged generative shoot with several nodes bearing several inflorescences at the upper nodes. In contrast, the other four *Phyllospadix* species have a short generative shoot with mostly one node bearing only one, occasionally two, inflorescences.

The inflorescence in the Zosteraceae is called the spathe, consisting of flowers formed on the flattened, spike-like axis known as the spadix and enveloped by a modified open leaf sheath known as the spathal sheath. In the monoecious *Zostera* and *Heterozostera*, two male flowers and one female flower are arranged alternately in two longitudinal rows (Fig. 12C and D), while in the dioecious *Phyllospadix*, either male or female flowers are arranged in two longitudinal rows. The male flower has one stamen with two bilocular anthers (theca). The female flower (gynoecium) has a single ovary with one ovule, a short style and two fine stigmata (Fig. 12C), which protrude to the surface of the spathal sheath along the overlapping wings at

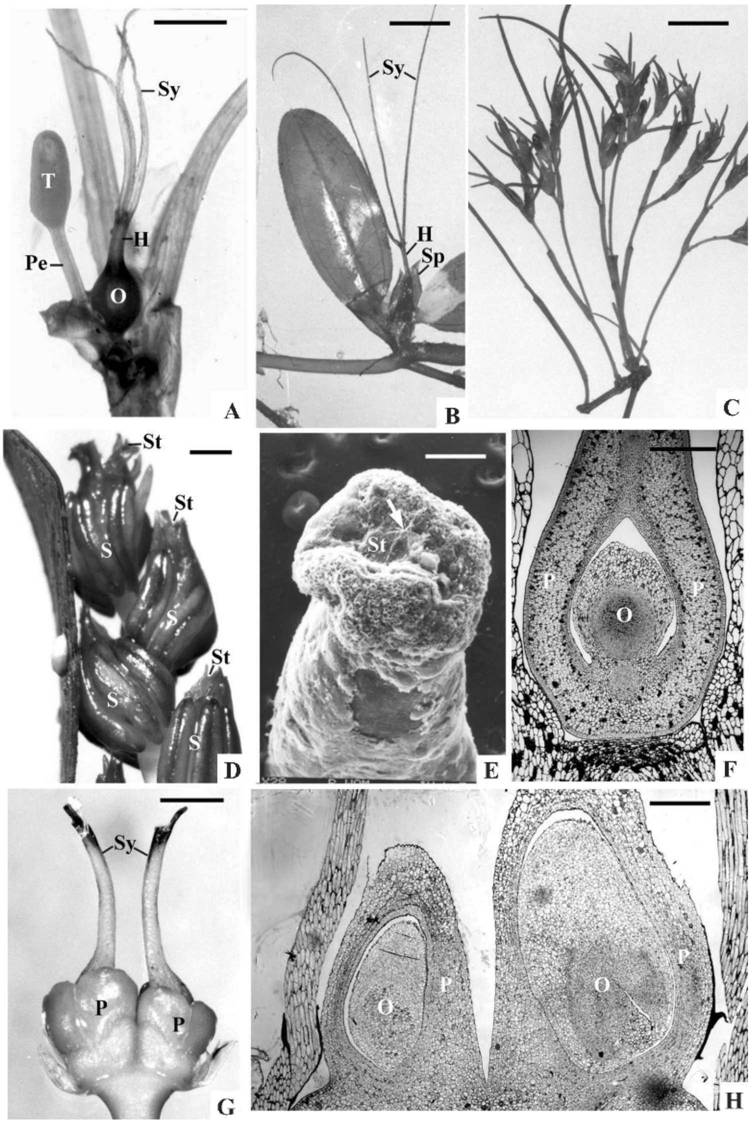

Fig. 11. Morphology and anatomy of female flowers. A. *Halophila decipiens* has a monoecious plant with male and female flowers on the same floral shoot. Note the elongating pedicel (Pe) with enlarging tepals (T) and an ovary (O) extending to a short hypanthium (H) and then to three elongated styles (Sy). Scale = 4 mm. B. *Halophila ovalis* has distinct cymose dioecious flower; the ovary is covered by two overlapping spathes (Sp), hypanthium (H) and three long styles (Sy). Scale = 8 mm. C. *Syringodium isoetifolium* has distinct cymose flowers. Scale = 25 mm. D. *Posidonia australis*. The spike-like racemose inflorescences are bisexual (hermaphrodite), each with three stamens and a single short stigma (St). Scale = 5 mm. E. *Posidonia robertsonae*. Fragments of thread-like pollen (arrow) attached to the stigma surface (St). Scale = 1 cm. F. *Posidonia australis*. The maturing flower has a basal ovary (O) surrounded by pericarp tissues (P). Scale = 330 μm. G. *Amphibolis antarctica*. Two female flowers form at the peduncle, stigmata broken off from styles (St) after anthesis, pericarp (P) yet to develop into a grappling apparatus. Scale = 3 mm. H. *Thalassodendron pachyrhizum*. The developing female flower has two ovaries (O); each is protected by pericarp tissues (P). Scale = 300 μm.

pollination. Furthermore, a peculiar triangular structure, known as the retinacula is present on the margins of the spadix, usually between two male anthers in monoecious plants (Figs. 12C and 13D) or between two flowers in dioecious plants. The structure has been interpreted as a bract or a reduced perianth (see Tomlinson, 1982; Soros-Pottruff and Posluszny, 1994). Retinaculae are well developed and may be associated with pollen and seed dispersal in *Phyllospadix* (Kuo, unpublished). However, they

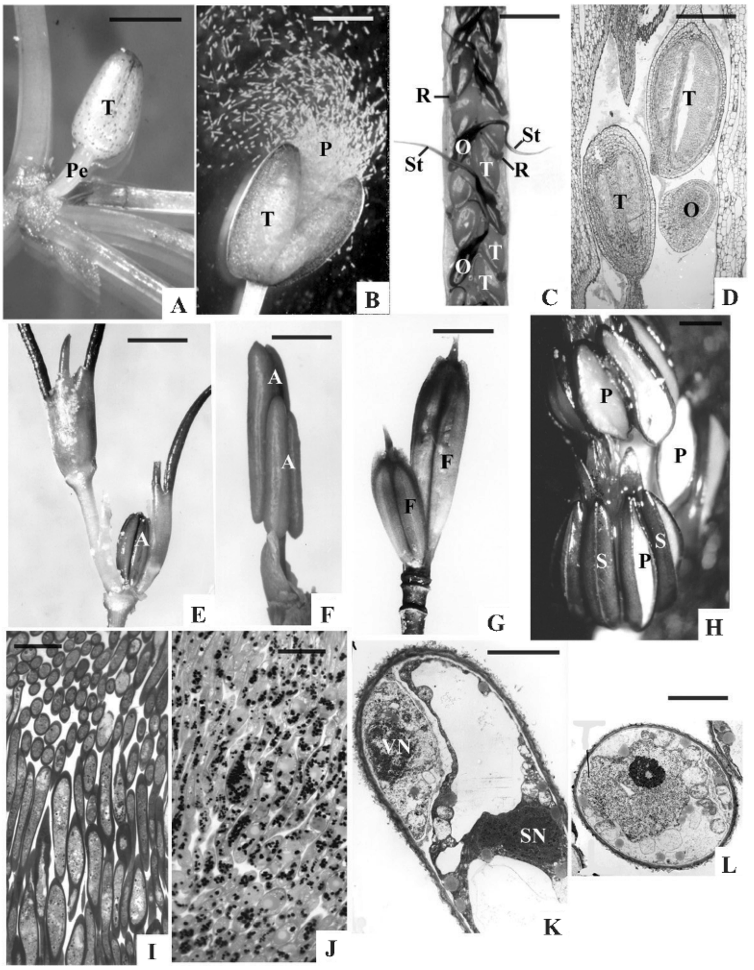

Fig. 12. Morphology, anatomy and ultrastructure of male flowers. A. *Halophila ovalis*. A maturing male flower with an extending pedicel (Pe) and a pigmented, swelling tepal (T). Scale = 4 mm. B. *Halophila beccarii*. The tepals (T) open to release pollen grains (P) in chains. Scale = 2 mm (Courtesy of Dr. B. Japar Sidik). C, D. *Heterozostera nigricaulis*. The monoecious flower has male and female flowers arranged in two rows; in each row a male flower with two thecae (T) alternates with a female with an ovary (O) and a long stigma (St). A small retinacula (R) occurs between two thecae. Scales C = 2 mm, D = 400 μm. E. *Syringodium isoetifolium*. Two anthers (A) form at the same level. Scale = 5 mm. F. *Halodule uninervis*. Two anthers (A) form at the different levels. Scale = 2 mm. G. *Thalassodendron pachyrhizum*. Each male flower (F) has two different developmental stages. Scale = 5 μm. H–L. *Posidonia australis*. Mature stamens (S) slit longitudinally to release a mass of thread like pollen (P), rich in starch. Each pollen has two vegetative nuclei (VN) and a sperm nucleus (SN). Scales H = 5 mm, I, J = 55 μm, K = 4 μm, L = 6 μm.

are small in *Heterozostera* (Fig. 12C) and *Zostera* subgenus *Zosterella*, and absent in *Zostera* subgenus *Zostera*. At anthesis, anthers slit longitudinally to release filamentous pollen. After anthesis, anthers detach from the spadix in monoecious flowers, but the entire male flowers detach from dioecious plants, while stigmata break off from styles in all species. It should be noted that the reproductive arrangement in the Zosteraceae is unique among seagrasses and the angiosperms. As there is no similar flowering pattern occurring in the terrestrial flowering plants, it may be suggested that the Zosteraceae have a very ancient marine/aquatic origin.

4. Posidoniaceae

In the Posidoniaceae, inflorescences are supported by long peduncles; they are racemose with leafy bracts; the ultimate units are spike-like, with several to 30 apparently naked flowers. The flowers are bisexual (hermaphrodite), each with three stamens and a female flower. The female flower consists of an oblong ovary containing one ovule (Fig. 11F) and a disc-like stigma with irregular lobes (Fig. 11E), but no perianth (Fig. 11D). The mature stamens split longitudinally and release thread-like pollen grains (Fig. 12H) and the remaining thecae persist after pollination.

5. Cymodoceaceae

The flowers of the Cymodoceaceae are usually solitary, and terminal on erect shoots (*Halodule, Cymodocea*) or their branches (*Amphibolis, Thalassodendron*). They are arranged as distinct cymose inflorescences in *Syringodium* (Fig. 11C). Each inflorescence consists of two morphologically identical flowers, which develop in the same way, except for the male flower in *Thalassodendron*, which has two developmentally different but morphologically identical flowers (Fig. 12G). The naked flowers are enclosed by leaf-like bracts. The male flower has two anthers fused back-to-back at the same height in all genera, while those in *Halodule* are at an unequal height (Fig. 12F). The female flower is sessile or with a short pedicel, has two free ovaries, each with a long simple style (Fig. 13F) (*Halodule*) or a short style which extends into two to three slender stigmas (Fig. 11G). The interpretation of floral morphology and structure in the Cymodoceaceae has been discussed by Kuo and McComb (1989) and McConchie and Knox (1989a).

6. Ruppiaceae

The inflorescence of *Ruppia* is formed as a terminal spike, which is enclosed by two subopposite foliage leaves. The peduncle elongates at anthesis, in most species elevating the inflorescence to or near the water surface. The inflorescence consists of two (rarely more) flowers located on opposite sides of the inflorescence axis. Each flower has two stamens with two thecae, and a gynoecium with (2-) 4 or more (up to 16) carpels, each bearing a single ovule (Lacroix and Kemp, 1997).

B. Floral Development

There are only a few studies on developmental morphology and anatomy of reproductive structures in seagrasses. Soros-Pottruff and Posluszny (1994) found that the developmental sequence is similar in the dioecious *Phyllospadix* and the monoecious *Zostera*. Initiation and development of the reproductive structures are acropetal along the length of the spadix. However, the female flower of *Phyllospadix* also contains the male floral units, which remain as minute residual structures; in contrast, there are no female reproductive units on the male plants. These authors concluded that, based on the more specialized habitat of *Phyllospadix*, possible pollination mechanisms with well-developed retinaculae and the presence of residual stamens on female inflorescences, the genus appears to be more primitive than *Zostera*. Tomlinson and Posluszny (1978) recorded that inflorescences in *Syringodium filiforme* are unique among the family Cymodoceaceae. It has an initially racemose and subsequently extensively cymose development, with terminal units referred to as 'flowers.' These authors suggested that its sympodial inflorescence is comparable with that of the Zannichelliaceae, although it is more variable and complex in the latter.

C. Floral Structure

1. Stigma Structure

According to McConchie and Knox (1989a), stigmas of the seagrasses belong to the 'dry type,' without free fluid on the surface; they have a hydrated proteinaceous surface layer and pellicle, functioning as a regulator of adhesion by hydration. However, the same authors (McConchie and Knox, 1989b) considered the stigma of *Posidonia* as belonging to the 'wet type,' although a secretion is not optically detectable, and a pellicle-like layer is present. Furthermore, *Enhalus, Thalassia* and *Halophila* have papillate stigmata with surface pellicles that possess esterase activity, with acid phosphatase accumulating below the cuticle. *Zostera* and *Amphibolis* are non-papillate, but *A. antarctica* has a thin pellicle covering the surface of the stigma.

2. Pollen Structure and Pollination

Pollination in all seagrasses is hydrophilous. The mature stamens of seagrasses form longitudinal slits

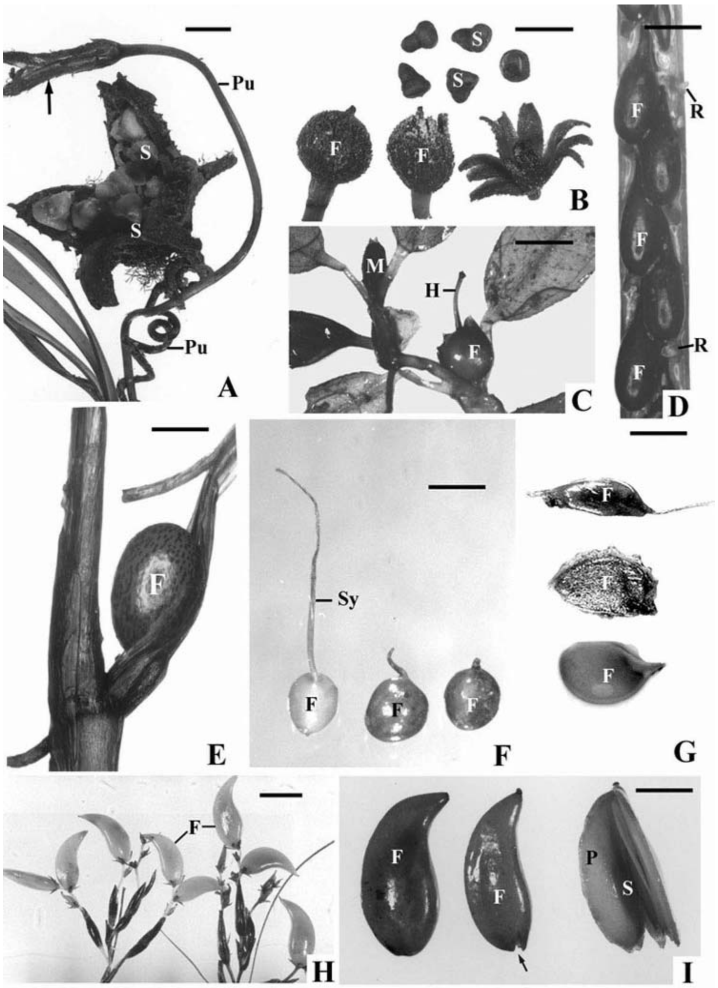

Fig. 13. Fruits. A. *Enhalus acoroides*. The mature fruit is carried by a coiled peduncle (Pu) and splits to release seeds (S). Note an immature female flower (arrow) is carried by a straight peduncle. Scale = 1 cm. B. *Thalassia hemprichii*. The mature fruit (F) opens to release several seeds (S). Scale = 1.5 cm. C. *Halophila capricorni*. The mature fruit (F) has a persistant hypanthium (H). Note the plant is monoecious and has male flower (M) forming on a different floral shoot. Scale = 4 mm. D. *Heterozostera tasmanica*. Maturing fruits (F) remaining on the spathe. Note the persistant retinaculae (R). Scale = 4 mm. E, F. *Halodule uninervis*. The maturing fruit is protected by leaf sheaths and has a long style (Sy). Scales E = 1mm, F = 2 mm. G. *Cymodocea* spp. Different species have different fruit morphology, Top: *C. serrulata*, Middle: *C. rotundata*, Bottom: *C. nodosa*. Scale = 4 mm. H, I. *Posidonia denhartogii*. Two to three fruits (F) are formed in each spike; the mature fruit splits (arrow) from the base of the pericarp (P) to release the seed (S). Scale = 1 cm.

and release pollen to the water for attachment to the stigma surface, either at the water surface or below depending on the species.

3. Pollen Types

Pollen in seagrasses consists of three major types based on their structure and pollination modes: Type a. The male flowers of *Enhalus* and *Ruppia* produce individual pollen grains; Type b. The male flower of *Thalassia* and *Halophila* releases pollen grains in long chains within mucilage tubes (Fig. 12B); and Type c. The remaining nine genera produce unique filiform pollen without exine (Fig. 12I–L) (McConchie and Knox, 1989a).

4. Hydrophilous Pollination

Enhalus is the only genus that releases entire mature flowers from the plant. These then float to the water surface to split and release pollen grains for pollination, a similar phenomenon also occurs in the freshwater aquatics *Vallisneria, Lagarosiphon* and *Hydrilla* in the same family. *Ruppia cirrhosa* and *R.* aff. *tuberosa* release individual boomerang-shaped pollen grains from submerged anthers to the water surface for pollination. However, *R. maritima* achieves a submerged pollination at the air-water interface of a gaseous bubble supplied from the air channels of the plant itself (Verhoeven, 1979). The pollen grain of *Ruppia* possesses both exine and intine as in terrestrial plants; the exine is reticulate, and not well developed over the ends of the grain.

Halophila and *Thalassia* have ellipsoid to spherical pollen grains forming chains within mucilage tubes, up to 80 μm long in *Halophila*, to achieve the same effect as filamentous pollen in the remaining seagrass genera. The pollen grain of *Halophila* possesses both exine and intine e.g. that of *H. decipiens* has a thin and unornamented exine covering a massive stratified intine (Pettitt and Jermy, 1975).

The remaining seagrass genera all have filamentous pollen (see Table 2, Ackerman, Chapter 4) but the disposition of the filamentous pollen within the anther loculus is different among genera. Pollen ultrastructural development in *Z. marina, Amphibolis* and *Thalassodendron* has been described by Pettitt and Jermy (1975) and Ducker et al. (1978), respectively. The latter authors observed that the first pollen mitosis occurs at the end of the young spore period immediately preceding the vacuolate period, in contrast to many terrestrial pollen events.

The pollen filaments lie parallel to the longitudinal axis of the anther in *Zostera*; irregularly coiled in *Halodule*; coiled but in no particular orientation in *Thalassodendron*; and coiled like a spring in *Amphibolis* (Ducker et al., 1977). Furthermore, the length of the filamentous pollen varies with the genus, *Zostera*—2700 μm; *Phyllospadix*—1000 μm; *Posidonia*—450 ± 140 μm and bow-shaped; *Halodule*—1000 μm; and *Amphibolis*—2840 ± 590 μm. Pollen of *A. griffithii* has a fine tip without branching and that of *A. antarctica* has a forked tip (see McConchie and Knox, 1989a).

The pollen wall of *Zostera capricorni, Heterozostera nigricaulis* (as *H. tasmanica*) and *Phyllospadix torreyi* has two microfibrillar layers with a clear demarcation. *H. nigricaulis* (as *H. tasmanica*) has an additional tubular inclusion in the outer wall layer. On the other hand, the pollen wall of *Posidonia australis* is not clearly stratified (layered). The mature pollen of *P. australis* has globular and tubular inclusions occurring in the outer region of the wall (Pettitt, 1984). The microfibrillar intine wall, ca. 0.6 μm, is covered with scattered lipids which, together with mucilage, may be important agents for regulating cohesion and releasing and dispersing pollen in seawater (McConchie et al., 1982).

5. Pollen Structure

All seagrass pollen is trinucleate regardless of whether it is granular or filamentous, and its nuclei are located centrally. *Posidonia australis* contains an elongated vegetative nucleus invariably in close apposition to the two ovoid sperm cells (Fig. 12K and L). These cells are bounded by irregular periplasm containing vesicles and their cytoplasm resembles that of the surrounding vegetative cells (Ducker et al., 1978).

The pollen from both granular and filamentous types is released from the submerged anthers and 'searches' through currents and waves (Verduin et al., 1996) for a submerged stigma. Cox (1988) and Ackerman (1995) discussed the two or three-dimensional 'search' by the pollen, particular in intertidal seagrass populations (see also Ackerman, Chapter 4). It is possible that pollination can also take place at the water surface in some intertidal seagrass genera such as *Halophila, Phyllospadix* and *Zostera*, because their mature reproductive organs often float at the water surface and pollen appears to be released during the highest tidal range.

6. Pollen–Stigma Interactions

For several species of the genera *Halodule* and *Zostera*, pollen germination may occur before the pollen contacts the stigma (Yamashita, 1976). On the other hand, Ackerman (1993) supported De Cock's (1978) observations that the pollen of *Z. marina* would not germinate without a 'stigmatic factor.' McConchie and Knox (1989a) described the interaction between the pollen and the stigma surface in *Zostera, Posidonia* and *Amphibolis.* Ultrastructurally, the proteinaceous film covering the pollen and the secretion from the stigma surface coalesce at each contact point, where the cuticle covering the stigma frequently becomes detached. Pollen germination then proceeds near but never at the point of stigma adhesion and penetrates the stigma between the receptive stigma cells (McConchie and Knox, 1989a,b). The stigma forms a collar of wall material that is raised to around the pollen tube in *Amphibolis*. On the other hand, in *Posidonia* the pollen tube is occluded by a plug of callose where it enters the pistil and the adjacent cells have callose deposited only at the wall adjacent to the pollen tube (McConchie and Knox, 1989a).

The entry of the pollen tube into the embryo sac has rarely been observed in any seagrass (see McConchie and Knox, 1989a; Ackerman, 1993). The pollen tube of *Cymodocea* enters through a micropyle and grows directly toward a synergid (Bornet, 1864), while that of *Amphibolis* grows between the cells of the nucellus before entering a synergid laterally from below.

Flowering in some seagrass species apparently does not occur often or has not been observed in the field (Marbà and Walker, 1999), and the male flowers in some species are rare (Williams, 1995). Therefore, the precise pollination and fertilization processes in these species remain unknown. It is also necessary to prove whether apomixy operates in certain seagrass species. Furthermore, knowledge of the barriers, if any, for preventing interspecific crossings leading to hybridization is still lacking (see also Waycott et al., Chapter 2 and Ackerman, Chapter 4).

D. Fruit and Seed

After fertilization, the ovary develops into a fruit in all flowering plants including seagrasses. In seagrasses, fruit development and fruit structure are as diversified as their flowering patterns and floral structures (see also Orth et al., Chapter 5). In general the seeds, ranging in the size from 0.3 to 0.5 mm in some *Halophila* species to more than 1–2 cm in *Enhalu*s, are furnished with a nutrition reserve and sink rather than float. The most remarkable structural feature in embryos of seagrasses is that the endosperm is short-lived and has been replaced by an enlarged hypocotyl (Tomlinson, 1982). In some seagrasses, the hypocotyl seems not only to serve as a nutrient storage for germination but also to provide a stabilizing device maintaining a constant seedling orientation.

1. Hydrocharitaceae

The floating female flowers of *Enhalus* are supported by elongated peduncles, which after pollination become coiled and retract the developing fruits down into the seagrass canopy. The mature fruit of *Enhalus* is a fleshy capsule ca. 6 cm long with a spinous surface. The capsule dehisces to release 2–6 angular seeds covered by a thin membrane (Fig. 13A). The embryo has a large hypocotyl, but the radicle is not developed. The fruit of *Thalassia* is globose, containing several angular seeds (Fig. 13B); the embryo has a large hypocotyl fused with the cotyledon (Fig. 14F). The fleshy capsule of *Halophila* has a persistent hypanthium (Fig. 13C) and contains several to numerous sub-spherical seeds, 0.5–2 mm in diameter depending on the species (Fig. 14D and E). Each seed possesses an embryo with a distinct leaf primordium protected by a coiled cotyledon, and an enlarged hypocotyl (Fig. 14D). The seed coat consists of several cell layers, the remains of the pericarp and a two-layered integument. The surface of the seed coat has distinct isometric reticulation and some micro-sculptures within the reticulation in most of the *Halophila* species (Fig. 14A) (Kuo and Kirkman, 1992, 1995) but appears as numerous fine protrusions in *H. tricostata* (Fig. 14B and C) (Kuo et al., 1993).

2. Zosteraceae

The fruit of *Zostera* and *Heterozostera* (Fig. 13D), is an achene with a scarious pericarp and a hard, fibrous endocarp as a ‘seed coat’. The seed of these genera is ellipsoidal and the embryo has an enlarged hypocotyl continuous with a large cotyledon (Fig. 14I and J). In contrast, the fruits of *Phyllospadix* are dark and rhomboid with two stiff inflexible arms covered numerous stiff bristles, forming a ‘grappling apparatus’ (Fig. 14K) that provides them with an excellent means to become entangled with marine algae, coralline algae in particular, and other organisms on the substratum (Gibbs, 1902). During seed development, the pericarp differentiates into a soft exocarp and mesocarp and a hard fibrous endocarp. The latter forms the main body of the two arms; it produces a large number of long cells with thick, lignified walled, which later become stiff inflexible bristles.

3. Posidoniaceae

In the Posidoniaceae, the fruits are soft with a fleshy pericarp, when shed. Each fruit splits longitudinally and releases a single developing seed (Fig. 13H and I). The embryo has an enlarged hypocotyl, a short radicle and is covered by a thin membrane (Fig. 14G).

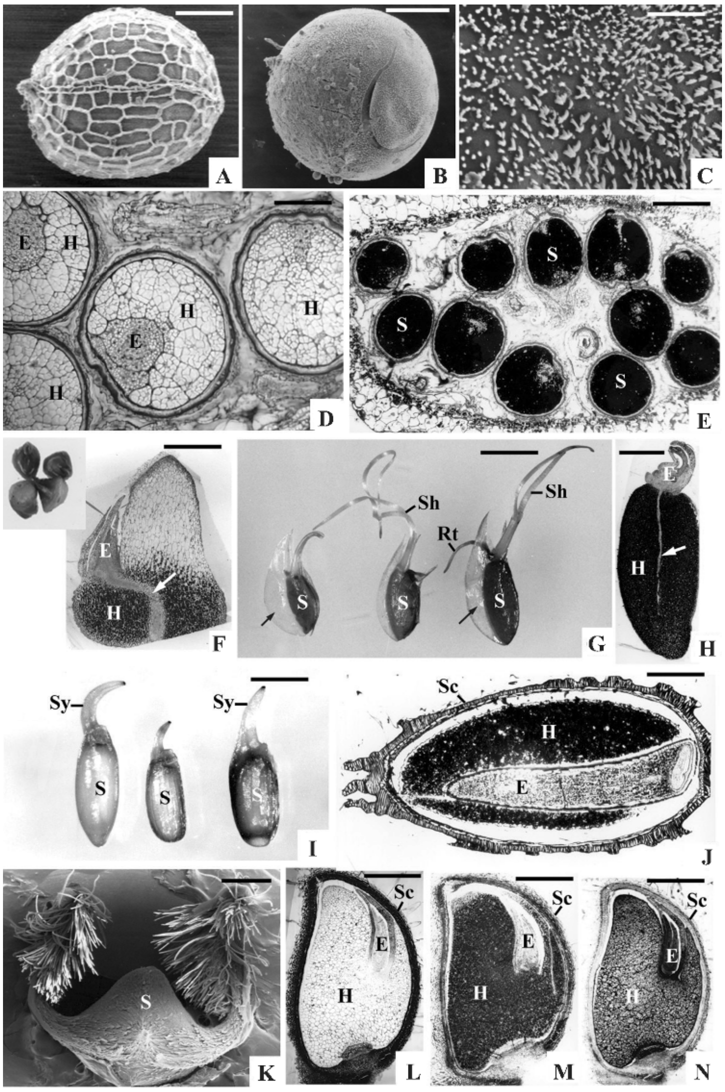

Fig. 14. Seeds. A. *Halophila ovalis*. The surface of seed coat has a distinct reticular pattern. Scale = 200 µm. B, C. *Halophila tricostata*. The surface of seed has numerous fine peculiar projections. Scales B = 200 µm, C = 20 µm. D, E. *Halophila ovalis*. Each oval *Halophila* seed has an embryo (E) and a large starch-rich (S) hypocotyl (H). Scales: D = 200 µm, E = 500 µm. F. *Thalassia hemprichii*. The triangular seed has an embryo (E) and an enlarged hypocotyl (H) in which starch is accumulated in the basal region. Note a provascular tissue (arrow) is running from the base of hypocotyl to the embryo. Scale = 2 mm. G, H. *Posidonia coriacea*. Seeds (S) with a membranous seed coat (arrows) and developing shoots (Sh) and new roots (Rt). An enlarged starch-rich hypocotyl (H) supports the embryo (E) development. A provascular tissue (white arrow) is also present. Scales: G = 1 cm, H = 500 µm. I, J. *Zostera marina*. Maturing seeds (S) with persistant styles (Sy). Mature seed has a distinct seed coat (Sc), a large embryo (E) and a starch-rich hypocotyl (H). Scales I = 3 mm, J = 500 µm. K–N. *Phyllospadix iwatensis*. Mature seed (S) has two arms with bristles; the fruit proper is protected by a complex seed coat (Sc). A small embryo (E) is rich in protein, without starch, and a large hypocotyl (H) is rich in starch. Scales: K–N all = 1 mm.

4. Cymodoceaceae

Cymodocea, Halodule and *Syringodium* in the family Cymodoceaceae produce indehiscent fruits with a stony pericarp (Fig. 13E–G) (den Hartog, 1970), but fruits of S*yringodium* retain only the stony endocarp, and the fleshy exocarp is lost during development (McMillan and Bragg, 1987). The embryo has a reduced radicle adjacent to an enlarged hypocotyl. The seed coats of *Halodule* are composed of flattened cells with annular thickening, and the oblong hypocotyls are composed of large,

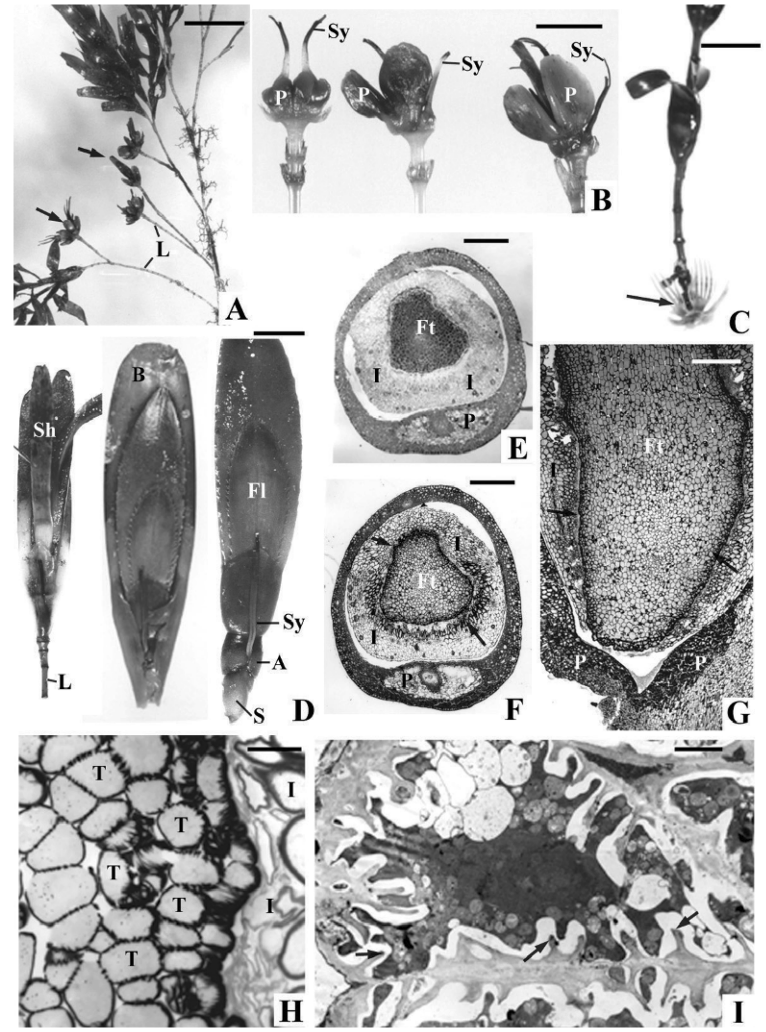

Fig. 15. Viviparous Reproduction. A. *Amphibolis antarctica*. Several developing seedlings (arrows) remain on later branches (L) of a parental plant. Scale = 2 cm. B. *Amphibolis griffithii*. Seen after removing bracts to show each peduncle carries two developing seedlings, each with an enlarging pericarp (P) and persistant styles (Sy). Scale = 1 cm. C. *Amphibolis antarctica*. The seedling has a grappling apparatus with bristles (arrow). Scale = 1 cm. D. *Thalassodendron pachyrhizum*. The viviparous seedling is germinated from a seed (S) and has an aril-like structure (A), style remains (Sy) and a shoot (Sh) is present containing several young leaves. The entire seedling is protected by an enlarged bract (B) and is attached to a lateral branch (L) of the parental plant. Scale = 500 μm. E–I. *Thalassodendron pachyrhizum*. The footing tissue (Ft) of the seedling is firmly surrounded by the integument (I) and then by the parent plant tissues (P). Footing tissue does not contain starch but is rich in protein. Numerous of transfer cells (T) with intensive wall ingrowths (arrows) occur in the outer layers of the footing tissues. Scales E, F, G = 500 μm, H = 50 μm, I = 2 μm.

polygonal cells that contain starch grains. The cotyledon and plumule are folded into a hypocotylary invagination along the line of wall separation. A radical hump or short radicle develops during germination in seawater (Bragg and McMillan, 1986).

In contrast to other genera in the Cymodoceaceae, *Amphibolis* and *Thalassodendron* produce unique viviparous seedlings (Fig. 15), which have not been observed in other aquatic plants. The embryo of *Amphibolis* has a long cotyledon, a short axis and no radicle, and it develops a leafy shoot remaining attached to the parent plant for about 8–12 months (Fig. 15A). There are four fleshy, herbaceous pericarp lobes initially growing at the base of the ovary (Fig. 15B); these become hard and have fine bristles united at the base, and form a 4-lobed 'comb' or 'grappling apparatus' (Fig. 15C) (Tepper, 1882a, b). This structure appears from the ovary wall late in the development of the flower, although its initiation is present prior to fertilization (see McConchie and Knox, 1989a). An abscission layer forms immediately below the comb and allows the release of the seedling, which is free until its grappling apparatus becomes caught in a substratum such as the fibrous base of *Posidonia* plant, algal turf or sand. Roots develop subsequently, and the grappling apparatus remains on the plant for another 6–12 months (Fig. 16F).

In *Thalassodendron*, the innermost bracts continue to develop after fertilization, and eventually enclose the carpels to form a false fruit (Cohen, 1939). Normally only one carpel is fertile, and a seed from this carpel germinates on the parent plant (see Kuo and Kirkman, 1987, 1990). Young seedlings at first have an aril-like structure that disappears at a later stage of seedling development. The seedling produces, firstly, an aberrant seedling leaf and a scarious seedling sheath, then several true foliage leaves and finally several root primordia (Fig. 15D) (Isaacs, 1969; den Hartog, 1970). The mature seedling detaches from the parent; separates from its protecting bract and sinks to the bottom. The remaining pericarps finally wash onto the shore.

5. Types of Seeds

Kuo and Kirkman (1996) classified three main types of functional seeds in relation to nutrient storage, seed coat structure and germination in seagrasses (see also Orth et al., Chapter 5). **Type a**. Seeds with hard pericarp or a distinct seed coat, e.g. *Zostera, Phyllospadix, Heterozostera, Cymodocea, Syringodium* and *Halodule*. However, seeds of both *Syringodium* and *Halodule* have thicker and harder coats than the seeds of the other genera and may have a longer dormancy. **Type b**. Seeds with a membranous coat, a modified pistil, as in *Posidonia*, and without a distinct dormancy, e.g. *Enhalus, Thalassia* and *Posidonia.* **Type c**. Seeds that neither have a normal distinct seed coat nor dormancy, but germinate on the parent plants (viviparous reproduction), e.g. *Thalassodendron* and *Amphibolis*: this unusual reproduction has not been reported in other aquatic plants. Histochemically, in Types a and b, seeds store large amount of starch and little protein in the hypocotyledonous tissue to be used during germination and seedling development (Fig. 14E, F, J and M). On the other hand, Type c seeds do not store starch and proteins, but the embryo obtains the necessary nutrients for seedling development direct from the parent plants through specialized transfer cells at the interface of seed and the parental tissue (Fig. 15F–I) (Kuo and Kirkman, 1996). These transfer cells have extended wall ingrowths and a plasmalemma, and are always associated with nutrient or solute transfer. The Type a seed has a distinct dormancy; while the Types b and c seeds do not.

The accumulation of nutrient including nitrogen, phosphorus and other macro- and microelements in *Posidonia* spp. (Hocking et al., 1980) and in *Enhalus* (Montaño et al., 1999) are in general comparable with those of terrestrial plants. Furthermore, there are numerous electron dense globoid crystals present in all tissues of the embryo of *Z. capricorni* and these contain P, Mg, K, Ca, Na and Cl (West et al., 1992) (see also Romero et al., Chapter 11).

6. Seed Numbers in the Annual and Perennial Seagrasses

As mentioned above only a few species of seagrasses are known as annual species, and the number of seeds produced by the annual and perennial plants varies greatly. For example, monoecious annual *H. decipiens* from Toro Point, Panama, had 13,500 seeds m^{-2} (McMillan, 1988), while the same species at Hardy Inlet, Western Australia, produced 176,880 seeds m^{-2} (Kuo and Kirkman, 1995). The dioecious annual *H. tricostata* at Fitzroy Island, in the Great Barrier Reef produced 70,000 seeds m^{-2} (Kuo et al., 1993). In comparison, the dioecious perennial *H. ovalis* produced about 480 seeds m^{-2} at Whitfords near Perth (Kuo and Kirkman, 1992). Plants of the annual *Z. marina* in Gulf of California, north western Mexico, have lifetime of about four months; they allocate all their resources into a seed production of up to 184,000 seeds m^{-2} while the perennial *Z. marina* in Baja California along the Pacific coast produces only 6300 seeds m^{-2} (Meling-Lopez and Ibarra-Obando, 1999, 2000).

E. Seedlings

As in all angiosperms, seeds of seagrass species normally germinate after a period of dormancy. However, the length of dormancy periods in seagrass

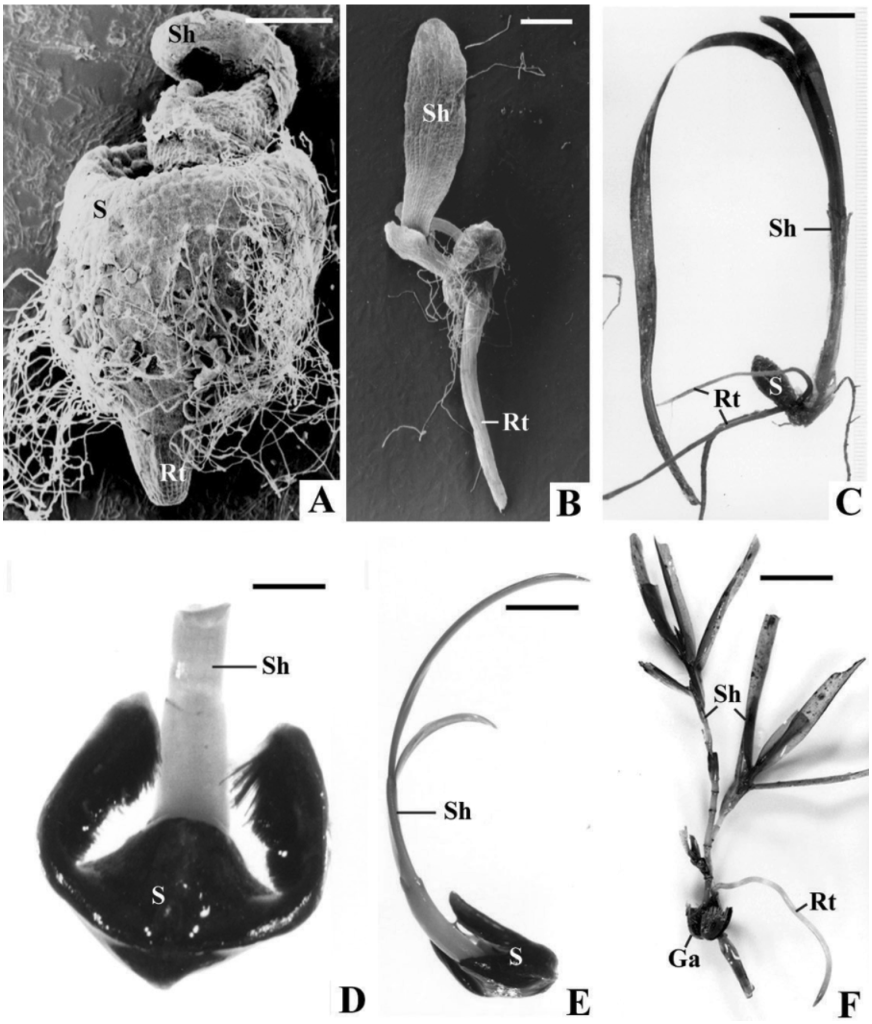

Fig. 16. Seedlings. A, B. *Halophila ovalis*. Note numerous root-hair-like structures developed on the surface of seed (S), which has an emerging shoot (Sh) and an emerging root (Rt). Scales A = 250 μm, B = 500 μm. C. *Posidonia australis*. Seed (S) remains on the well-established seedling, which already has developing shoots (Sh) and roots (Rt). Scale = 2 cm. D, E. *Phyllospadix iwatensis*. New shoots (Sh) emerge from the distal end of the seed (S) but roots emerge much later. Scales D = 1.75 mm, E = 3.5 mm. F. *Amphibolis griffithii.* A seedling with a grappling apparatus (Ga), a well-developed shoot (Sh) and an emerging root (Rt). Scale = 1 cm.

seeds depends on seed coat structure and is not associated with annual or perennial species nor whether they are temperate or tropical species. As described in the above section, the species having seeds with membranous seed coats (*Enhalus, Thalassia* and *Posidonia*) do not have a distinct dormancy period and their seeds germinate as they are being released from the parent plants. ‘Seeds’ of viviparous species (*Amphibolis* and *Thalassodendron*) germinate immediately after fertilization on the parental plants. Seeds from other seagrass genera have medium to hard seed coats and subsequently have distinct dormancy periods from a few months to a few years.

1. Hydrocharitaceae

Enhalus and *Thalassia* have a loose membranous seed cover which slips off easily; a profuse growth of anchoring hairs is developed from the lower surface of the seed. The detailed morphological development of *Halophila* seedlings has been described for several species including *H. spinulosa*

(Birch, 1981); *H. engelmanni* (McMillan, 1987; Jewett-Smith and McMillan, 1990); *H. decipiens* (McMillan, 1988; McMillan and Soong, 1989; Kuo and Kirkman, 1995); *H. tricostata* (Kuo et al., 1993) and *H. beccarii* (Muta Harah et al., 1999, 2000). The seedlings of all *Halophila* species display unusual early growth of 'hypocotylar hairs' or 'anchoring hairs' from the surface of the hypocotylar collar, which appear to anchor the seed before the emergence of the radicle (Fig. 16A and B). A similar phenomenon also occurs in fresh water monocotyledonous seedlings (Kaul, 1978), in some aquatic dicotyledonous seedlings and in a few terrestrial plants (Arber, 1925).

2. Zosteraceae

Anatomical studies on seed and seedling development in *Zostera marina* and *Z. japonica* have been published by Taylor (1957a, b) and Yamashita (1973). The rhomboid fruit of *Phyllospadix* (Fig. 14K) has a dormancy period of about 6 weeks. During germination, the shoots emerge first (Fig. 16D and E) and roots usually emerge more than six months later (Kuo et al., 1990b). Nutrient reserves in the *Phyllospadix* hypocotyl disappear about 4 months after germination.

3. Posidoniaceae

Fruits of Australian *Posidonia* mature in the early summer, 3 months after anthesis (Fig. 13H and I) and germinate as soon as being released without a distinct dormancy period (Fig. 14G). Roots are produced shortly after. Starch and nutrient reserves in the hypocotyl exhausted by eight months after germination, but the hypocotyl (seed) may still be attached to young plants (Fig. 16C) for more than 2 years (Kuo and Kirkman, 1996). On the other hand, seeds of *P. oceanica* germinated in culture media within 15–18 days with up to 96.2% germination rate, and no less than 75% of the seedlings survived and grew continuously for 10 months (Balestri et al., 1998).

4. Cymodoceaceae

In the tropical species *Cymodocea rotundata*, germination can occur throughout the year. Seeds of *Halodule* may be dormant for long periods, possibly extending over many years, while those of *Syringodium* show only short-term dormancy. However, seeds of *Halodule* and *Syringodium* are able to germinate for more than 3 years after they have been released from the parent plant. The longevity of seeds of these species may well exceed that of other seagrasses (McMillan, 1983a).

Finally, it should mentioned that Orth et al. (2000) reviewed seed dormancy, seed bank and germination of seagrasses and the possible applications of this knowledge for the conservation and restoration of seagrass beds (see also Orth et al., Chapter 5).

V. Water Movement in Seagrass Leaves and Roots

By using apoplastic tracers, Barnabas (1988, 1989, 1991, 1994a) showed that sea water freely enters from the medium and moves amongst the leaf blade and root tissues of *Thalassodendron ciliatum* and *Halodule uninervis*. However, water movement is restricted by the suberin of the vascular bundles in the blades and by the hypodermis and endodermis in the roots. Furthermore, in contrast to leaf blades, leaf sheaths have a distinct 'suberin-like' cuticle that prevents seawater entering the sheath tissue and acts as a protection of the meristem tissues and developing leaves. As mentioned in Section III.C.1, Tyerman (1989) showed that the leaf sheath in *Posidonia australis* provides for the developing leaf an (lower) osmotic environment different from the seawater environment, which the leaf experiences when it emerges from the leaf sheath. Indeed, Arai et al. (1991) showed that spherical protoplasts isolated from young leaf blades of several seagrass species, i.e. *Zostera marina, Z. japonica* and *Phyllospadix iwatensis*, which were protected from seawater by the leaf sheath, had little resistance to seawater. Nonspherical protoplasts from mature leaf blades of the same species were resistant to wide ranges of osmotic potential and salinity.

It has been demonstrated biochemically and physiologically that the plasmalemma (PM) of leaf cells in seagrasses plays an important role in osmoregulation. The salt-tolerant H^+-ATPase generates an electrochemical membrane potential in the seagrass plasmalemma preventing Na^+ from entering into the cytoplasm (Pak et al., 1995). Several intracellular ATPase enzymes including PEPC for CO_2 fixation, ATPase in mitochondria and ATPase in the tonoplast, are not salt-tolerant thus osmoregulation may not take place within the cytoplasm in *Z. marina* cells. It should be stressed that (PM) H^+-ATPase and (PM) Na^+/H^+ are found neither in freshwater *Vallisneria* nor the terrestrial monocotyledon rice *Oryza*, despite both species sharing similar anatomical features as seagrasses, indicating that possession of this important enzyme permits seagrasses to grow in high Na^+ concentrations (Muramatsu et al., 2002). The role of ion transport is also discussed by Larkum et al. in Chapter 14 in relation to photosynthetic inorganic carbon uptake by leaves.

VI. Morphological, Anatomical and Ultrastructural Modifications in Relation to Environmental Conditions

Several seagrasses show considerable morphological variations from a wide range of geographic distribution. Some species have different reproductive strategies under different environmental circumstances. For example, *Zostera marina* is largely perennial in the sublittoral, but in the intertidal belt many populations appear to be annual. The *Z. marina* population in the Sea of Cortez is annual; its development is totally restricted to the cooler season, while along the Pacific coast of the same latitude the species is fully perennial. Other morphological variations concern the broad-leaved *P. oceanica* from Algiers (Semroud et al., 1992), *Halodule wrightii* from southern Brazil (Creed, 1999), *Halodule* spp. from Malaysia (Japar Sidik et al., 1999) and *Halophila spinulosa* with three leaflets instead of two at the nodes of the erect stem in Malaysia (Japar Sidik et al., 2000). Further it has become clear from transplant experiments that morphologically similar plants of the same taxon may be physiologically different, with relation to tolerating low or high temperatures, salinity fluctuations, day length, etc.

Iyer and Barnabas (1993) demonstrated that leaf epidermal cells of low-salinity *Zostera capensis*, compared to seawater plants, had larger central vacuoles; fewer chloroplasts; reduced plasmalemma area; fewer mitochondria; thinner walls; reduced extra cytoplasmic volume; and symplastic connections with mesophyll cells. Cell walls of high-salinity plants histochemically show a stronger acidity gradient indicating a pH driven anion exchange mechanism in the wall. Similar results were found for *Ruppia maritima* (Jagels and Barnabas, 1989).

Light intensity also has effects on seagrass morphology and anatomy. Abal et al. (1994) showed that plants of *Zostera capricorni* Aschers. grown under high light conditions (50–100% light) had smaller shoots, higher biomass and productivity, larger air lacunae, but less negative $\delta^{13}C$ values, lower nitrogen content, less chlorophyll and more ultraviolet light absorbing pigment than plants grown under low light conditions (<20% light). Olesen et al. (2002) also discussed light capture efficiency with water depth for *Cymodocea nodosa*.

Cooper and McRoy (1988) found that numbers of fibers per bundle and bundle frequency are relatively constant in the three co-existing *Phyllospadix* species: *P. torreyi, P. serrulatus* and *P. scouleri* at different tidal heights at Cape Arago, Oregon, U.S.A., but leaf and epidermal cell thickness of *P. torreyi* and *P. serrulatus* significantly decrease as tidal height increases.

Seagrasses cannot grow to such great depths as their algal counterparts and there has been much discussion of this difference (Duarte, 1991), an observation made by Hutchinson (1975) for hydrophytes in general. It has been related to the extra physiological/biochemical load of having roots and rhizomes (Hemminga, 1998; Olesen et al., 2002) but it has also been ascribed to poor ability to change anatomical adaptations such as air lacunae (Beer and Waisel, 1982). In this respect, it is noteworthy that aquatic freshwater angiosperms have rarely been found at depths greater than 10 m; compared with them many seagrasses show a better performance. Schwarz and Hellblom (2002) showed that chloroplasts of *Halophila stipulacea* become clumped in shallow water. West (1990) showed that leaf width and leaf length of *Posidonia australis* had low variability between shallow (0.5 m) and deep (8.5 m) sites; however, unit frond weight was significantly higher in shallow sites and leaf area per shoot was significantly lower in deep sites. Some seagrass species can grow in clear deep water by reducing the leaf thickness, hypodermal fiber frequency and grana density in chloroplasts, and by increasing the phenolic contents in mesophyll cells in *P. oceanica* (Colombo et al., 1983). On the other hand, *Halophila decipiens* and *Thalassodendron ciliatum* can grow from the intertidal zone to a depth of more than 60 m, apparently without any morphological or anatomical modification (Kuo and den Hartog, 2000). The relationship between seagrass morphology/anatomy and water depth also has been discussed by Larkum et al. in Chapter 14.

VII. Discussion and Concluding Remarks

This chapter has attempted to illustrate how all modern seagrasses have several morphological and anatomical modifications, both vegetative and reproductive, which differentiate them from terrestrial plants. But many of these morphological and anatomical modifications also occur in freshwater plants (Arber, 1920; Sculthorpe, 1967) and must be interpreted as adaptations to the aquatic environment. These features include leaves having a thin cuticle; small epidermal cells with thick walls; concentrations of chloroplasts in the epidermal cells; a lack of stomata, an enlarged aerenchyma system and a reduced xylem accompanied sometimes by reduced mechanical tissues. In many cases, seagrasses retain many functional, morphological and anatomical features of terrestrial plants. These features include the presence of suberin or lignin or similar structures that restrict apoplastic pathways in bundle sheath cells in the leaves, and having a hypodermis and an endodermis in the rhizomes and roots. While there are few or no particular structures in seagrass that can be identified as unique in terms of structural adaptation to the marine environment, there is a suite of characters, which together can be taken as representative of seagrasses. These include strap-shaped leaves and anatomical reinforcement to resist wave action, adaptation of leaves to carry out photosynthesis in a seawater environment, osmotic adjustment and other adaptations within the leaf blade and leaf sheath, modifications to rhizomes and roots for different substrata, pollination by hydrophily, reduction in the layers of the pollen wall and several unique features associated with seed formation and dispersal mechanisms.

Furthermore, the morphology and anatomy of vegetative and reproductive organs also varies among different taxa suggesting that seagrasses probably neither evolved from a common ancestor nor through the same evolutionary pathways, nor in the same geological period. Most of those freshwater or terrestrial cousins no longer exist. On the other hand, after establishment in marine habitats, 'seagrasses' had little pressure to modify further their morphological and anatomical structures to meet new physiological or biochemical requirements (Larkum and den Hartog, 1989).

The greatest physiological and biochemical adaptation is probably the conversion on HCO_3^- in seawater into CO_2 presumably by anhydrase enzymes at the outer tangential walls of epidermal cells and also the presence of a proton pump at the plasmalemma of seagrass leaves. However, this applies also to most freshwater plants.

So far, the salt-tolerant H^+-ATPase has only been demonstrated biochemically and physiologically in the leaf plasmalemma of *Z. marina* that possesses wall ingrowths in the blade epidermis. It will be interesting in future to see whether this pump is a common feature of seagrasses and whether it is connected to the control of sodium concentration.

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Chapter 4

Sexual Reproduction of Seagrasses: Pollination in the Marine Context

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I. Introduction

A discussion of sexual reproduction in seagrasses should begin with an examination of their origin and include a comparison with their closest freshwater relatives (i.e. the comparative method). There were no marine plants until angiosperms colonized marine coastal waters sometime in the Cretaceous, which is the earliest date of seagrass fossils (i.e. $>100 \times 10^6$ years ago; den Hartog, 1970; Larkum and den Hartog, 1989). Prior to that time, bacteria and protists (i.e. algae) were the only marine photosynthetic organisms, as embryophytic plants had evolved earlier as a terrestrial group (Niklas, 1997; Dawes, 1998). The anatomical, morphological, and molecular evidence indicates that seagrasses evolved from freshwater ancestors (Arber, 1920; Sculthorpe, 1967; den Hartog, 1970; Tomlinson, 1982; Les et al., 1997), which are also polyphyletic in origin having evolved multiple times (Cook, 1996a, 1998). In this context, cetaceans are the zoological equivalent of seagrasses, and the analogy continues in that both groups are relatively depauperate systematically compared to their terrestrial functional analogues. Specifically, seagrasses represent ~0.5% of the total marine flora and 0.02% of all angiosperms (Dawes, 1998), with 50–60 species in 13 genera (see below) found in the familiar aquatic plant families Hydrocharitaceae, Cymodoceaceae, Posidoniaceae, and Zosteraceae within the Alismatales order of the monocotoledons (den Hartog, 1970; Tomlinson, 1982; Cook, 1996a; Dawes, 1998; den Hartog and Kuo, Chapter 1; Waycott et al., Chapter 2). Molecular phylogenies have identified at least three clades within the seagrasses depending on how one defines the group (Les et al., 1997), which strengthens the argument that these plants are polyphyletic and thus represent a functional group (i.e. a grade of evolution).

Given the polyphyletic origin of the seagrasses, we would expect significant differences in their reproductive biology. Concomitantly, the possession of similar apomorphies among the clades would be evidence of convergence related to the fact that similar evolutionary pressures were faced during the origin and continued evolution of these clades. Arber (1920) perceived these pressures as: (1) toleration towards a saline medium; (2) the power of vegetating while wholly submerged; (3) the knack of developing a sufficiency of anchoring roots to withstand the action of waves and tides; and (4) the capacity for hydrophilous pollination; and den Hartog (1970) included a fifth: (5) the need to disperse in the marine context. Indeed, there are a large number of morphological and physiological characters in seagrasses that support these views (Table 1). The shared occurrence of many of these characters in freshwater plants speaks to the freshwater origin of seagrasses, whereas the uncommon and/or unique characters speak to their evolutionary innovation. Principle among these innovations in reproductive characters are submerged flowers, filamentous pollen, and ssubmarine pollination (Table 1; Ackerman, 1995, 2000), which are dealt with in detail below. It has been argued that the "capacity for hydrophilous pollination" in the marine context has limited seagrass biodiversity, but it is more likely that the lack of allopatric isolating mechanisms in coastal environments, especially as compared to freshwater plants, is the cause, given the convergence in

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Table 1. Selected vegetative and reproductive characters of seagrasses compared to freshwater angiosperms.

Seagrass character	Occurrence in freshwater plants	Reference
(A) Vegetative character		
Ribbon-shaped, terete, or lanceolate leaves (no whorled or dissected leaves)	Common	den Hartog (1970); Tomlinson (1982)
No stomates, thin cuticle, chloroplasts in epidermis	Common	Tomlinson (1982)
Salt excretion through epidermis	Uncommon	Tomlinson (1982)
Root and rhizome systems	Common, but not as well developed	Stevenson (1988)
Ion and water uptake from roots	Common, but at higher rates	Pedersen and Sand-Jensen (1993)
Reduced xylem	Common	Esau (1977); Tomlinson (1982)
Lacunar gas system	Common	Esau (1977); Tomlinson (1982)
(B) Reproductive character		
Submerged flowers	Rare (excluding cleistogamous species)	Ackerman (2000)
Highly reduced flowers	Uncommon (moderate reduction common)	Ackerman (2000)
Dioecy	Uncommon	den Hartog (1970)
Spherical to spheroidal pollen	Common	Ackerman (2000)
Filamentous or functionally-filamentous pollen	Absent	Pettitt (1984); Ackerman (2000)
Surface pollination (rare in seagrasses)	Uncommon	Ackerman (1995, 2000)
Submarine pollination (common in seagrasses)	Rare	Ackerman (1995, 2000)
Endosperm absent in mature embryo	Common	Tomlinson (1982)
Floatation as a means of diaspore dispersal	Common	Orth et al. (Chapter 5)
Geocarpy	Absent	Inglis (2000); Orth et al. (Chapter 5)

aforementioned reproductive characters (Ackerman, 1998). Clearly a review of the reproductive features of seagrasses as they relate to pollination mechanisms would be of value. It is the purpose of this chapter to provide such a review by building upon earlier efforts (e.g. den Hartog, 1970; Tomlinson, 1982; Pettitt, 1984; Kuo and McComb, 1989; McConchie and Knox, 1989a; Ackerman, 1995, 2000; Walker et al., 2001; Okubo et al., 2002) and extending into the realm of comparative evolutionary ecology.

II. Defining Seagrasses

The lack of a single common ancestry for seagrasses has led to flexibility in the definition of what constitutes a member of this group. It would seem reasonable to follow the direction of den Hartog (1970) who concluded that a seagrass was a plant that satisfied the five criteria defined above. This would limit the group to 13 genera (*Enhalus, Thalassia, Halophila, Amphibolis, Cymodocea, Halodule, Syringodium, Thalassodendron, Posidonia, Heterozostera, Phyllospadix, Nanozostera* (Tomlinson and Posluszny 2001), and *Zostera;* note that Les et al. (2002) recommend collapsing *Heterozostera* and *Nanozostera* into *Zostera*), even though den Hartog (1970), Tomlinson (1982), and others (e.g. Les et al., 1997) acknowledge that a number of other genera can be found in estuarine and inland conditions with high salinity (e.g. *Althenia, Lepilaena, Potamogeton, Pseudalthenia, Ruppia, Zannichellia*). *Ruppia* and *Zannichellia,* are included here for comparative purposes as they are often considered to be seagrasses (den Hartog and Kuo, Chapter 1), but it will become evident that their reproductive biology is quite unlike true seagrasses (*sensu* den Hartog, 1970; see Table 2; cf. Waycott et al., Chapter 2).

III. Evolutionary Ecology

There has always been some question as to the role of sexual reproduction in seagrasses given that they are a largely rhizomatous or clonal group. This latter attribute is a characteristic that is associated with aquatic plants, and has sometimes been

Table 2. Selected reproductive characters in seagrass genera (data from Arber, 1920; den Hartog, 1970; Ducker et al., 1978; McConchie 1982; Pettitt 1980, 1984; Tomlinson 1982; McConchie; Knox, 1989a; Guo et al., 1990; Inglis 2000; Smith and Walker 2002).

	Reproductive ecology			Staminate flower			Carpellate flower		Diaspore	
Genus (# sp)	Mode	Dicliny	Arrangement	Anthers	Pollen (dimensions)	Exine	Carpels	Texture	Fruit	Seed
Hydrocharitaceae										
Enhalus (1)	Surface	Dioecious	Inflorescence solitary	3 stamens, 6 tepals, free floating flowers	Spherical, few large (150–175 μm)	Present	3 sepals, 6 styles	Papillate stigma	Fleshy, ovoid with 8–14 seeds	Not dormant, no endosperm, obconical, few in number
Thalassia (2)	Submarine	Dioecious	1–4 solitary on inflorescence	8–12 stamens	Spherical (80–100 μm) in long chains	Present	Hypanthia with 2 long stigmas	Papillate	Fleshy, globose	Not dormant, no endosperm, conical, several large
Halophila (14)	Submarine	Monoecious and dioecious	Unisexual solitary flower	3 stamens pedicilate	Ellipsoidal (80 × 40 μm) in linear pollinium	Absent	Long style and hypanthia with 2–6 stigmas	Papillate	Fleshy, globose, geocarpy	Dormant, no endosperm, globose, several minute
Cymodoceaceae										
Amphibolis (2)	Submarine	Dioecious	Solitary and terminal naked flower on short lateral shoots	2 united anthers, stalked	Filiform (3–5000 × 20 μm)	Absent	2 carpels, each with 3 long stigmas	Non-papillate	Germination on plant	Viviparous, no endosperm, seedling has comb-like appendage
Cymodocea (4)	Submarine	Dioecious	Solitary and terminal naked flower	2 united anthers, stalked	Filiform (2000 × 10 μm)	?	2 carpels each with 2 long stigmas	Non-papillate	Laterally compressed, geocarpy	Dormant, no endosperm
Halodule (8)	Submarine	Dioecious	Solitary and terminal flower	2 united anthers at different heights, stalked	Filiform (1000 μm)	Absent	2 carpels, each with a long stigma	Non-papillate	Stony pericarp, geocarpy	Dormant, no endosperm
Syringodium (2)	Submarine	Dioecious	Cymose inflorescence	2 united anthers, stalked	Filiform	?	2 carpels, each with 2 long stigmas	Non-papillate	Ellipsoidal, stony pericarp	Dormant, no endosperm
Thalassodendron (2)	Submarine	Dioecious	Terminal, two flower inflorescence on short shoots	2 completely united anthers stalked	Filiform (5000 × 20 μm)	Absent	2 carpels, each with 2 long stigmas	Non-papillate	False fruit, fleshy bracts	Viviparous, no endosperm, free floating seedling

(*continued*)

Table 2. (*Cont.*)

	Reproductive ecology			Staminate flower			Carpellate flower		Diaspore	
Genus (# sp)	Mode	Dicliny	Arrangement	Anthers	Pollen (dimensions)	Exine	Carpels	Texture	Fruit	Seed
Zannichelliaceae[a]										
Zannichellia (1)	Submarine	Monoecious	1–2 flowers in leaf axil	Naked with 1–2 theca	Spherical (23–28 μm)	Present	Group of funnel-shaped stigmas	Non-papillate	Achene, dorsal ridge	No endosperm
Ruppiaceae[a]										
Ruppia (2–10)	Surface	Monoecious	Inflorescence	2 stamens	Chevron (90 × 30 μm)	Present	Number of funnel-shaped stigmas	Non-papillate	Achene	No endosperm
Posidoniaceae										
Posidonia (9)	Submarine	Bisexual	Bisexual flowers on cymose inflorescence	3 stamens	Filiform (500–1000 μm)	Absent	1 carpel with disc-shaped lobed stigma	Non-papillate	Fleshy, free floating	Not dormant, no endosperm, elliptical
Zosteraceae[b]										
Heterozostera (1)	Submarine	Monoecious	Unisexual on inflorescence (spathe-spadix)	1 stamen with 2 free thecae, long retinacules	Filiform	Absent	1 carpel with 2 stigmas	Non-papillate	Ovoid–ellipsoidal	Dormant, no endosperm, finely striated
Phyllospadix (5)	Submarine and surface	Dioecious	Unisexual on inflorescence (spathe-spadix)	1 stamen with 2 free thecae, retinacules	Filiform (1500 μm)	Absent	1 carpel with 2 stigmas	Non-papillate	Crescent shaped with fibrous endocarp	Dormant, no endosperm,
Nanozostera (8)	Submarine and surface	Monoecious	Unisexual on inflorescence (spathe-spadix)	1 stamen with 2 free thecae, short retinacules	Filiform	Absent	1 carpel with 2 stigmas	Non-papillate	Ellipsoid	Dormant, no endosperm, smooth, ribbed, ridged
Zostera (4)	Submarine and surface	Monoecious	Unisexual on inflorescence (spathe-spadix)	1 stamen with 2 free thecae, no retinacules	Filiform (2700 × 7.5 μm)	Absent	1 carpel with 2 stigmas	Non-papillate	Ellipsoid	Dormant, no endosperm, smooth, ribbed, ridged

[a] Taxon included for comparative purposes (i.e. not always considered a seagrass).

[b] Note that Les et al. (2002) recommend collapsing *Heterozostera* and *Nanozostera* into *Zostera*.

ascribed to them (Grace, 1993). Apparently this may be the case in dicotyledons where most of the 30 rhizomatous families (i.e. ~10% of total families) are semi-aquatic or aquatic, but not in the monocotyledons where a high proportion (i.e. 70%) of all monocotyledon families are rhizomatous (Grace, 1993). Seagrasses, as monocotyledons, possess many characteristics of the Alismatidae including clonal growth. Regardless of the reason for a rhizomatous existence, the necessity of sexual reproduction remains a valid question given the advantages of asexual reproduction (Jackson et al., 1985): i.e. (1) it maintains and propagates "good" genotypes through growth and dispersal via fragmentation (e.g. Campbell, 2003); (2) it removes the needs for the clones of the opposite sex in the dioecious populations; (3) it provides multiple versions of the same genotype in the event of mortality (i.e. escape in numbers); and (4) it removes the real costs of reproduction (Obeso, 2002). Similarly, there are a number of advantages for sexual reproduction (e.g. Williams, 1975) that include: (1) the maintenance of genetic variation through meiosis and fertilization, which is essential for natural selection; (2) the masking of deleterious genes, and perhaps the generation of Sisyphean genotypes that can colonize new habitats or niches; (3) the deposition of a dormant stage (e.g. seeds) that provides an escape in time; and (4) the facilitation of dispersal, which is a fundamental process that follows sexual reproduction. In other words, sexual reproduction is important for the long-term stability of populations under dynamic change (Silander, 1985; cf. Rasheed, 1999), and also in the short-term continued presence of populations that are annual due to excessive heat or ice scouring (e.g. Keddy and Patriquin, 1978; Meling-Lopez and Ibarra-Obando, 1999). Moreover, genetic analyses have revealed high outcrossing rates in a number of seagrasses (Ruckleshaus, 1995; Waycott and Sampson, 1997; Reusch, 2000; Waycott et al., Chapter 2), which speaks to the importance of pollination in natural populations. Given these findings, there can be little doubt of the role of sexual reproduction in seagrasses.

The evolutionary ecology of sexual reproduction in seagrasses is not unlike that of other plants with abiotic pollination (Ackerman, 2000). In this context, a number of characteristics are present, presumably to facilitate outcrossing and thus limit the probability of self pollination (Charlesworth, 1993). Specifically, there is a separation of carpellate and staminate reproductive structures (1) in space, in the case of the nine genera with dioecious species and/or (2) in time via dichogamous pollination (i.e. phenological separation between pollen reception and pollen release; usually protogyny), in the case of the four monoecious genera (*Halophila, Heterozostera, Nanozostera,* and *Zostera*; *Posidonia* is bisexual with perfect flowers; see Table 2; Tomlinson, 1982; Pettitt, 1984; Les et al., 1997). It is also important to note that considerable biochemical evolution occurred in the transition to hydrophily given that the pollen and stigmatic surfaces are exposed to wet conditions (Pettitt, 1984; McConchie and Knox, 1989a). In addition to problems associated with osmotic balance, water may disrupt pollen germination cues, interfere with chemical cues on stigmatic surface, and transport material that may foul surfaces. Consequently, most aquatic plants reproduce above the water surface using entomophily (insect pollination; ~242/380 genera) and anemophily (wind pollination; ~119 genera) similar to their terrestrial relatives (Ackerman 1995, 2000; Cook, 1996a; Philbrick and Les, 1996). Indeed, despite the relatively high proportion of wind-pollinated aquatics, only four genera have evolved anemophily from an entomophilous ancestry (Cook, 1988, 1996b). A very small fraction of the aquatics are hydrophilous (~19 genera) and pollinate without animal vectors (abiotic pollination) either on (ephydrophily) or in (hyphydrophily) the water (Ackerman, 1995, 2000). Ephydrophily is common in freshwater plants and in shallow coastal habitats in the case of *Enhalus acoroides* (L.f.) Royle and sometimes when the reproductive organs of intertidal seagrasses may lie on the water surface (Tomlinson, 1982; Ackerman, 2000). Submarine pollination is, however, the dominant pollination mode in the other 12 genera of seagrasses and is limited to a few freshwater genera (Cook, 1996a; Ackerman, 2000). Ackerman (2000) summarized the ecological factors in a surface pollination syndrome to include largely clonal plants that are dioecious or diclinous, in which spheroidal pollen is released under moderate flows in shallow habitats leading to reasonably high outcrossing rates. The ecological factors in a submarine pollination syndrome include mostly dioecious clonal plants with dicliny (protogyny) in which filiform pollen is released under flowing conditions in coastal marine habitats leading to high outcrossing rates.

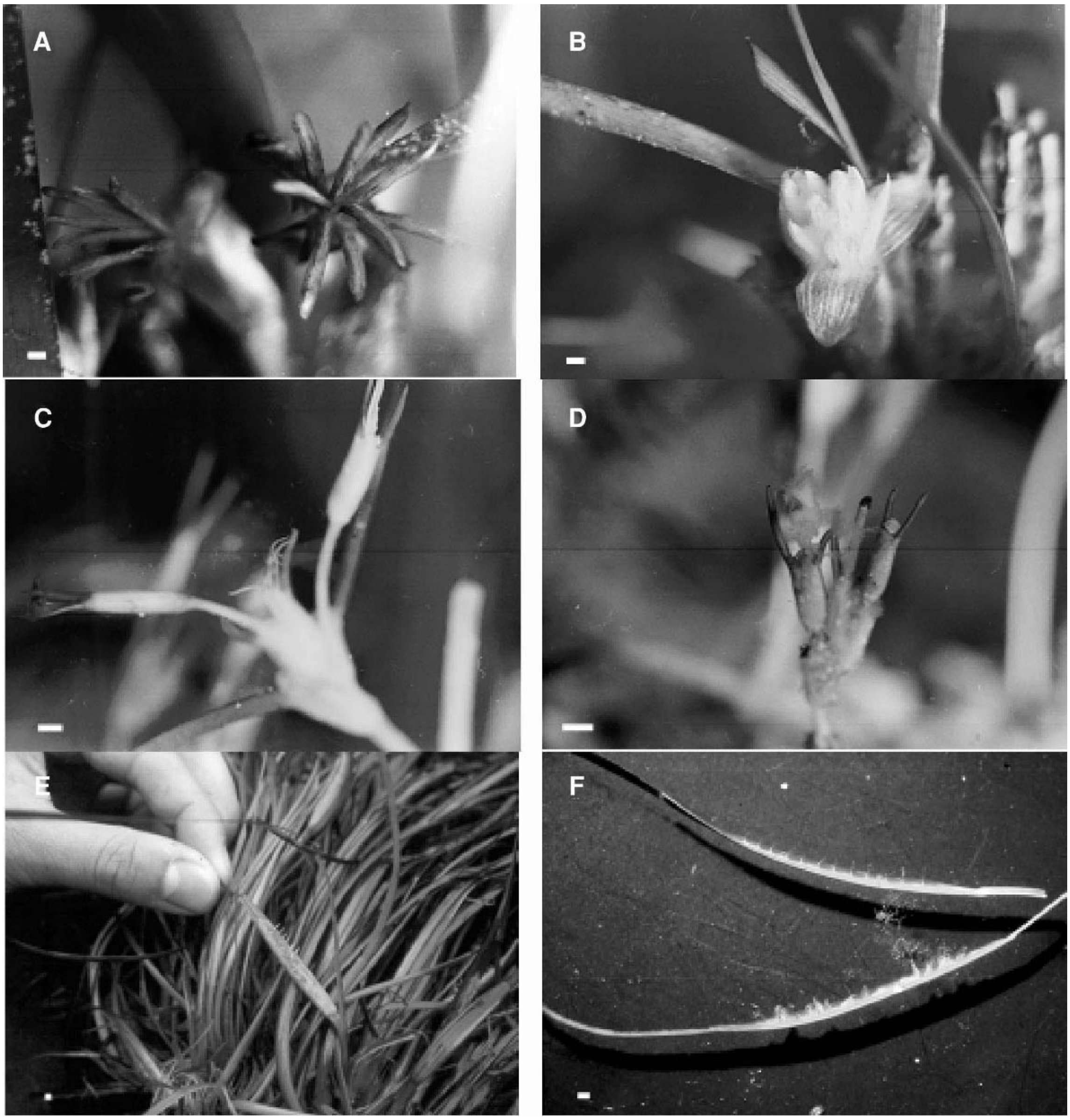

Fig. 1. Reproductive organs of selected seagrasses. (A) *Thalassia testudinum* female inflorescence; (B) *T. testidinum* male inflorescence; (C) *Syringodium filiforme* female inflorescence, note the paired stigmas of the central flower; (D) *S. filiforme* male inflorescence, note the dehiscence of pollen in the leftmost flower (normal elongation of the filament has been disrupted by removal from the field); (E) *Phyllospadix scouleri Hooker*—female inflorescence with receptive stigmas that have emerged from within the spathe; (F) *Zostera marina* inflorescences with exerted stigmas (upper inflorescence) and in anthesis of pollen (lower inflorescence) (scale bar = 2 mm).

IV. Morphological Patterns: Reproductive Organs

The reproductive organs of seagrasses are generally highly reduced, which reflects both their evolutionary origin and the specialized nature of these plants for submerged abiotic pollination (Fig. 1; Arber, 1920; Sculthorpe, 1967; den Hartog, 1970; Tomlinson, 1982; McConchie and Knox, 1989a; Ackerman, 1995, 2000; Kuo and den Hartog, 2001; Kuo and den Hartog, Chapter 3). Nine of the thirteen genera are dioecious with largely solitary male and female flowers, and the remaining four genera (note that *Halophila* has both dioecious and monoecious species) are monoecious with either perfect flowers (*Posidonia*) or unisexual flowers in cymose inflorescences (*Halophila*) or in flattened inflorescences with spathe-spadix arrangements (Zosteraceae; Table 2; see also Fig. 12C and D, Kuo and den Hartog, Chapter 3). With the exception of *Enhalus* and *Thalassia*, which share many features with their freshwater relatives (e.g. *Vallisneria*), the flowers are drab rather than showy, and perianth parts are absent or bract like in appearance (den Hartog, 1970; Tomlinson, 1982). For example, the solitary unisexual flowers of *Cymodoceae* are "naked", being composed essentially of two united anthers on a filamentous stalk in the case of staminate flowers, and two free carpels each with two slender styles (three in *Amphibolis*) (see Fig. 12, Chapter 3).

The spatial location and orientation of the reproductive organs is critical from the perspective of submarine pollination. Specifically, the fluid dynamic release and/or capture of pollen will vary according to whether anthers or carpels are located basally or distally on the plants, given the velocity gradient near the bottom and the plant canopy (i.e. benthic and canopy boundary layers; Okubo et al., 2002). In this situation, there is an advantage to elevating anthers away from the bottom to facilitate pollen dispersal in the faster moving fluid, while placing stigmas close to the bottom or within axils of bracts or vegetative material to facilitate the reduction and redirection of water flow for pollen capture (cf. Niklas, 1992). This appears to be the case in a number of genera like *Thalassia, Halophila,* and *Cymodocea*, and reaches an extreme in *Amphibolis* where some anthers can detach and float to the surface where pollen can disperse through the water column (McConchie and Knox, 1989b). This latter example should not be confused with the obligate surface pollination of *Enhalus*, where detached free-floating male flowers encounter female flowers on long spirally coiled peduncles (den Hartog, 1970; Tomlinson, 1982). The situation becomes more complex when reproductive organs of diocecious (*Syringodium, Phyllospadix*) or monoecious genera (*Posidonia, Nanozostera, Zostera*) are organized into inflorescences that extend into or above the top of the plant canopy. In these cases, the fluid dynamically induced movements of the plants are likely to affect the dispersal and capture of pollen through waving sweep-like motions (i.e. monami; Ackerman and Okubo, 1993) analogous to wind pollination in grasses and other herbaceous plants (Niklas, 1992; Ackerman, 2000). Recognizing this, it should be noted that much research is needed to confirm these patterns, which extend from fluid dynamic principles in wind-pollinated plants (Niklas, 1992; Ackerman, 2000).

Staminate and carpellate flowers appear to be organized into a number of different patterns that do not appear to match with systematic patterns (i.e. Hydrocharitaceae vs. other seagrass families) or patterns in pollen morphology (spherical vs. filamentous; see below; Table 2). In the first type, the carpellate inflorescence of *Enhalus* and *Thalassia* are trimerous with subtending perianth parts, which are easily identified as "flowers" by the nonspecialists (Fig. 1A). The solitary carpellate flowers have long bifid stigmas, which are papillate (for additional information pertaining to properties of stigmas see McConchie and Knox, 1989a; Table 2). The second type of floral arrangement includes a number of genera (*Halophila*, *Amphibolis*, *Cymodocea*, *Halodule*, and *Thalassodendron*) with solitary, highly-reduced "naked" flowers that can be on short pedicels close to the seafloor. As noted above, the staminate flowers are usually stalked with two united anthers (three in *Halophila*), and the carpellate flowers usually have two carpels each with a long slender bifid stigma (*Halodule* has one stigma; *Amphibolis* has three stigmas), which is non-papillate (*Halophila* is papillate; Tomlinson, 1982). It is important to note that the stigmas, which are the receptive surfaces of the styles, may be long; i.e. ~9 mm in *Amphibolis* and ~30 mm in *Cymodocea* (Tomlinson, 1982; McConchie and Knox, 1989b; see Fig. 11, Chapter 3). A third pattern is seen in *Posidonia*, which has a racemose inflorescence with perfect flowers consisting of a single disk-shaped irregularly lobed stigma and three stamens (Tomlinson, 1982; McConchie and Knox, 1989b; see Fig. 11, Chapter 3). It is important to note that this type of stigmatic surface is distinct among the seagrass, which have slender stigmas, and is more reminiscent of some freshwater species (Table 2). The final pattern is seen in the remaining genera in which unisexual flowers are borne on long branched cymose inflorescences (*Syringodium;* Fig. 1C and D) or on long branched inflorescences with a spathe-spadix configuration (*Heterozostera*, *Phyllospadix*, *Nanozostera*, and *Zostera*; Fig. 1E and F). In *Syringodium* the stalked staminate flowers have two united anthers and the carpellate flowers have two free carpels each with a bifid stigma. In the Zosteraceae, the carpellate flowers, consisting as a single ovulate carpel with a short bifid stigma, are arranged linearly on one side of the spadix and these are bounded on either side by one thecae of each pair of the staminate flower (den Hartog, 1970; Tomlinson, 1982; Fig. 12C and D, Chapter 3).

V. Pollen

Pollen characteristics are among the most unique features in seagrasses (Table 1). As in the pollen of other aquatic plants, there is a reduction in pollen ultrastructure and in exine ornamentation, which is absent in a number of taxa (Table 2; Sculthorpe, 1967; Pettitt and Jermy, 1975; McConchie, 1982; Pettitt, 1984; McConchie and Knox, 1989a). In the Zosteraceae there are two (or three) stratified microfibrillar layers in the pollen wall, slight stratification in the pollen wall of the Cymodoceaceae, and no stratification in the pollen wall of the Posidoniaceae (McConchie, 1982; Pettitt, 1984; McConchie and Knox, 1989a). Associated with these ultrastructures are gross pollen morphological patterns that include spherical, ellipsoidal, and filiform (filamentous or confervoid) shapes (den Hartog, 1970; Tomlinson, 1982; Ackerman, 2000), the latter extending to 5 mm lengths (∼20 μm diameter) in *Amphibolis* with curved or forked tips (Ducker and Knox, 1976; McConchie and Knox, 1989a). Systematically, spherical pollen shapes are restricted to *Enhalus* and *Thalassia*, and ellipsoidal pollen shapes are found in *Halophila*, which are all in the Hydrocharitaceae, whereas filiform pollen are found in the remaining 10 genera, which are in the Cymodoceaceae, Posidoniaceae, and Zosteraceae (i.e. Potamogetonales of Tomlinson, 1982; Table 2; Fig. 12, Chapter 3).

Notwithstanding these differences in pollen shape, there is a strong tendency for pollen to be transported as filaments in the submarine pollinated genera (*Thalassia* and *Halophila*; Ackerman, 1995, 2000). In *Thalassia*, spherical pollen can be linked in mucilaginous chains (present inside the thecae) or can germinate precociously, which leads to a filamentous shape as first noted by Bowman (1922; also see Pascasio and Santos, 1930). In *Halophila,* four ellipsoidal pollen grains are contained and transported within a filamentous structure (Balfour, 1879; Kausik and Rao, 1942). An examination of pollen development is useful in this context as it provides insight into the nature of pollen with filamentous shapes (Ackerman, 1995). Monocotyledons undergo successive pollen development, which leads to “cross T” configured tetrads in *Thalassia*, “linear” tetrads in *Thalassia* and *Halophila*, and “square isobilateral” tetrads in the Zosteraceae and Cymodoceaceae (presumably, *Posidonia* is also of the latter type; Fig. 2; Pettitt, 1984; Iwanami et al., 1988). The interesting aspect of the development in *Halophila* is that the linearly arranged tetrad forms the functional unit (i.e. a pollinium). It is not known whether there is any difference in the contribution of pollen from the cross T or linear tetrads of *Thalassia* to the filamentous chains, but chains contain more than four pollen grains (i.e. >1 tetrad). An examination of the development of filiform pollen (Fig. 3) is equally revealing in that the origin of filiform pollen is polyphyletic (Ackerman, 1995, 2000). In this case, filiform pollen arises from the elongation of microspores prior to reductive division in the Zosteraceae (Fig. 3; Rosenberg, 1901a; Pettitt and Jermy, 1975; Stewart and Rüdenberg, 1980), but following reductive division in the Cymodoceaceae (Fig. 3; Yamashita, 1976; Pettitt, 1981; Pettitt et al., 1981; Pettitt, 1984). Lastly, it is instructive to note that the orientation of filiform pollen within anthers varies systematically, with parallel orientation in the Zosteraceae (Dudley, 1893; Rosenberg, 1901a; Pettitt and Jermy, 1975; Ackerman, 1993), and spiral or irregular orientation in the Cymodoceaceae (Bornet, 1864; Pettitt, 1976; Yamashita, 1976; Ducker et al., 1978). It would be insightful to ascertain which of these latter two patterns occurs in the Posidoniaceae. Regardless, the data indicate that filiform pollen morphologies are convergent in the seagrasses either as filamentous (i.e. filiform) or functionally filamentous structures (Ackerman, 1995, 2000).

VI. Reproductive Patterns

Patterns in the reproduction of seagrasses may provide insight into the cues that induce floral development, trigger flowering, and control the flowering process (i.e. phenology) within individuals and populations. These patterns will vary with biotic factors related to the genetics, physiology (growth regulators), and conditions of the local population, and with abiotic factors related to light (photoperiod, red to far red ratios), temperature, and latitude (Pettitt, 1984; Rathcke and Lacey, 1985; see Smith and Walker, 2002). Lastly, geographic location, ease

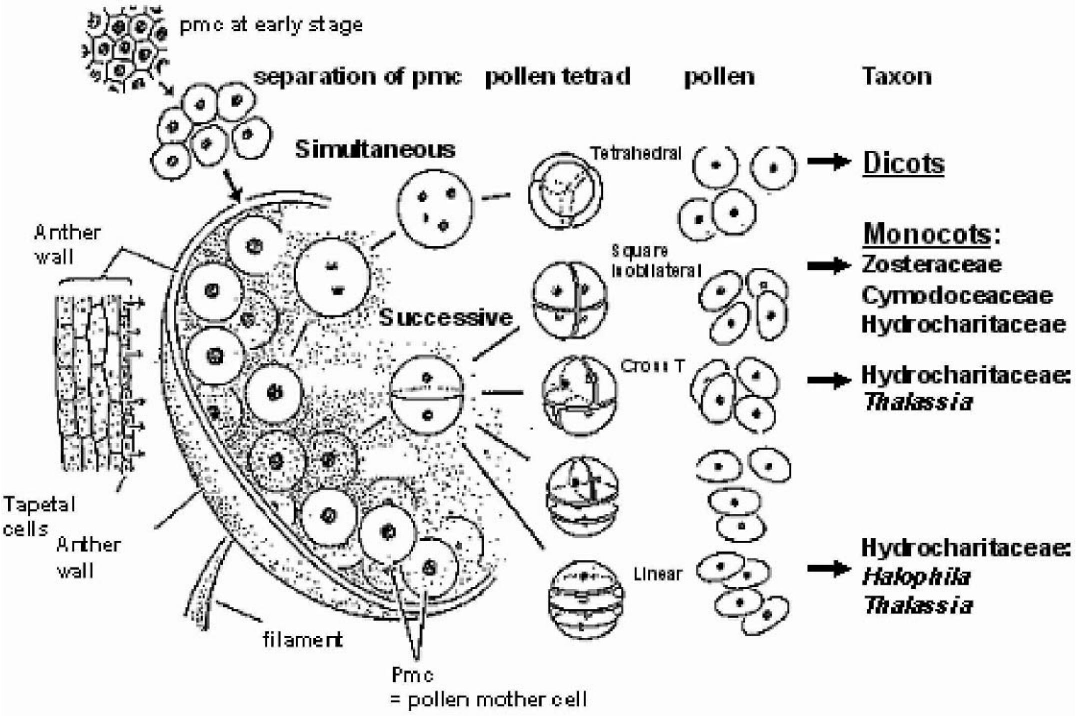

Fig. 2. Microsporogensis and microgametogenesis with reference to successive pollen development in seagrass genera (modified from Iwanami et al., 1988).

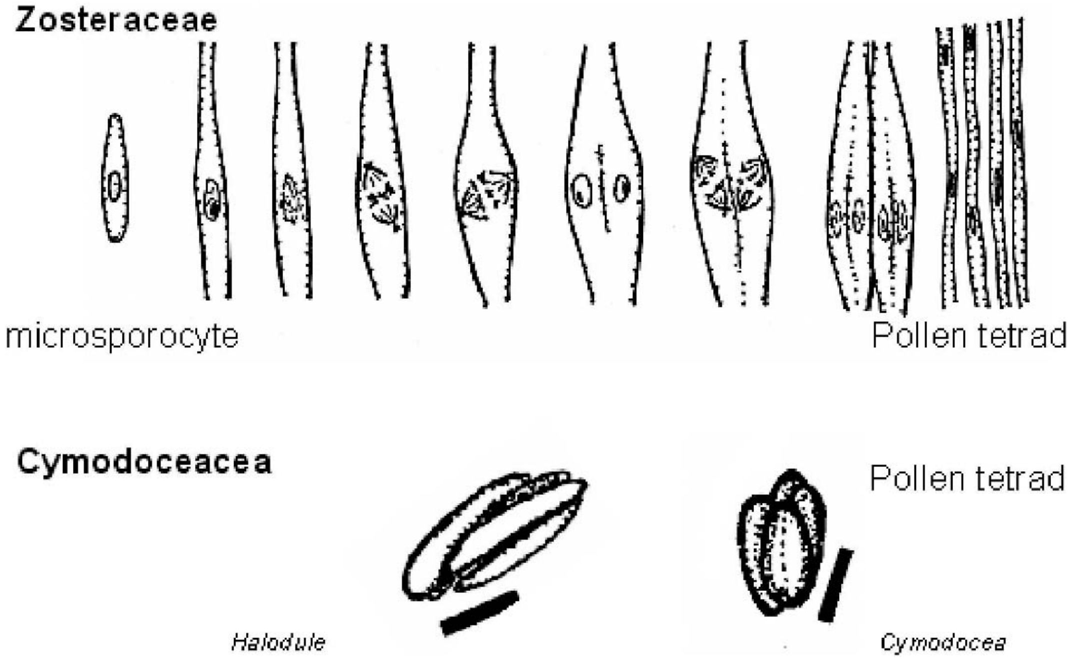

Fig. 3. Pollen development involves an elongation of the microspores prior to reductive division in the Zosteraceae and post reductive division in the Cymodoceae. Scale bar = 20 μm (after Rosenberg, 1901a; Harada, 1948; Stewart and Rüdenberg, 1980).

of access to sites, and societal factors such as interest, and number of scientific personnel has also influenced the understanding of local and regional conditions (Walker et al., 2001). Consequently, there are geographic regions, such as the North Atlantic, Mediterranean, and parts of the North Pacific coasts, where phenological patterns are well described, but the majority of coasts, including the regions of high diversity, are less well known (Walker et al., 2001).

Coincident with large-scale phenomena is the spatial and temporal variation in flowering phenology that exists on local scales. This is most evident in taxa in which flowering is periodic, rare and/or in which reproductive material has not been described (e.g. *Cymodocea angustata* Osterfeld, *Halodule beaudettei* (den Hartog) den Hartog, *Halodule bermudensis* den Hartog, *Halodule emarginata* den Hartog, *Halophila johnsonii* Eiseman; Kuo and den Hartog, 2001).

Notwithstanding these gaps in understanding, there are taxa in which the phenological patterns are well known. For example, the phenology of *Zostera marina* L has been described (de Cock, 1980), and reproductive shoots can represent from 0 to 100% of a given population with variation existing due to photoperiod and water temperature (Phillips et al., 1983; Olesen, 1999). Walker et al. (2001) provide a detailed review of this topic from a geographic perspective, which reveals that most genera are reproductive in the spring and summer (i.e. increase in day length and warmer water temperatures) (e.g. *Thalassia, Halophila, Syringodium, Halodule, Cymodocea, Thalassodendron, Phyllospadix, Nanozostera, Zostera*), a number flower in the fall and winter (i.e. decrease in day length and cooler water temperatures) (e.g. *Amphibolis, Posidonia, Heterozostera*), and one genus is reproductive throughout the year (*Enhalus*), although there are exceptions especially for tropical species.

VII. Pollination

Whereas aspects of pollination in seagrasses have been addressed by a number of authors (Sculthorpe, 1967; den Hartog, 1970; Tomlinson, 1982; Pettitt, 1984; Kuo and McComb, 1989; McConchie and Knox, 1989a; Walker et al., 2001; Okubo et al., 2002), this treatment will follow a functional approach and focus on pollination mechanisms, following from Ackerman (1995, 2000). As indicated above, seagrasses are among a limited number of taxa that pollinate underwater using water currents, the exception being *Enhalus*, which as discussed previously is ephydrophilous (see below for detailed description). Submarine pollination is restricted to the coastal marine environment, where there is more energetic and regular water motion (e.g. tidal and wind-generated currents) than in freshwater systems, where movements vary greatly and are a function of basin morphometry (Nixon, 1988; Schindler, 1991; Kalff, 2002). There can be little doubt that some shallow intertidal seagrass populations may be exposed to air during low tides, however, subtidal populations are, by definition, never exposed (see den Hartog, 1970; Ackerman, 1986). This may be less evident during spring tides when tidal exchanges are the largest, however, as indicated above, latitudinal and depth gradients in flowering phenology (Phillips et al., 1983) limit surface pollination to local situations. It is also important to note that pollen released at the surface will be maintained on the surface unless sufficient external force is expended to overcome the surface tension (see Ackerman, 1997b). Cox and co-workers (reviewed in Cox, 1988) have used a mathematical model (random search theory) to assert that selection pressures for surface pollination have led to the evolution of filiform pollen in seagrasses and arrays of pollen in freshwater plants (the so-called elongate search vehicle). Whereas the mathematical models are correct, they are not applicable to seagrass pollination in a mathematical or biological sense because wind and water currents have directional components (i.e. particle trajectories are not recurrent), pollen rotate in the boundary layers around flowers (i.e. not perpendicular to the pathline; see Fig. 4 and 5, below), and filiform pollen is found only in seagrasses and not in related freshwater plants (see treatments in McConchie and Knox, 1989a; Ackerman, 1995).

Notwithstanding the fact that surface pollination does occur in some situations, it is clear that filiform pollen has evolved for pollination underwater under dynamic flow conditions due to mechanical advantages of increased pollen length. This advantage is revealed when filiform shapes are compared to spherical shapes under flowing conditions where a particle’s motion is due to fluid translation, fluid rotation, and fluid deformation (Fig. 5; Visser, 2001). Velocity gradients (boundary layers) exist around flowers and inflorescences under

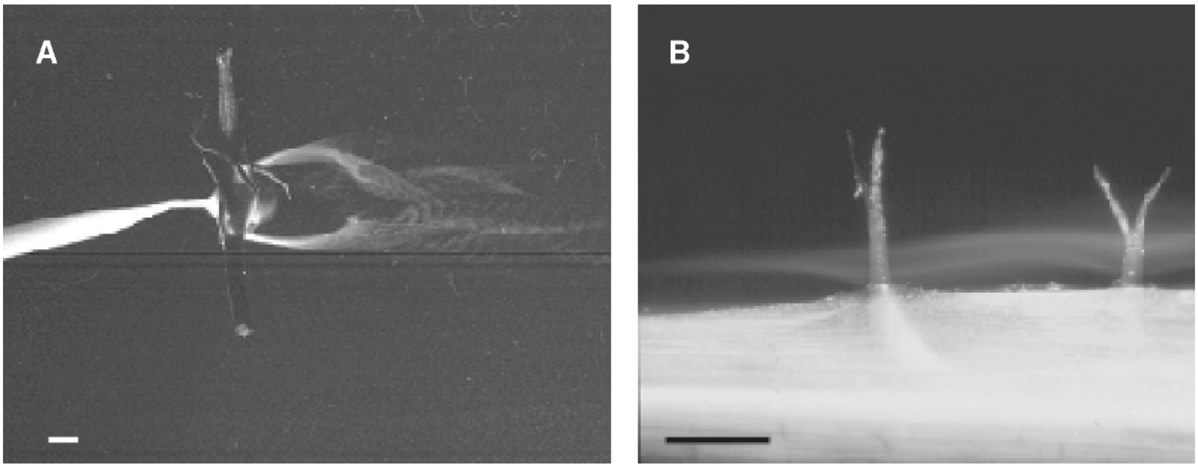

Fig. 4. Flow visualization around seagrass carpellate flowers and inflorescences at an average chamber velocity of ~3 cm/s using the flow chamber described in Ackerman (1997a,b). Flow is from left to right. (A) Flow around a *Syringodium filiforme* carpellate inflorescence in side view using milk. Note the recirculation zone immediately downstream of the inflorescence; (B) Flow around two *Zostera marina* flowers in side view using fluoroscein dye. Note the smooth uninterrupted flow in the flow field around the flower (scale bar = 2 mm).

flowing conditions that lead to increasing velocity from the flower (Ackerman, 1997a). The shear in these velocity gradients cause particles to rotate as they are transported downstream, however the rotation is greater for filiform particles due to the larger axial force that they experience (i.e. they extend over a larger range of velocities in the velocity gradient; Fig. 5; Ackerman, 1997b). Pollen capture can occur via direct interception within a streamline, rotation of pollen within 1/2 a pollen length of the stigma, or via redirection in the boundary layer around inflorescences and flowers (Ackerman, 1995). This process is three-dimensional (Goldsmith and Mason, 1967) and occurs under dynamic conditions.

Pollination mechanisms are presented for each seagrass genus, and the dearth of observations on the release, transport, and capture of pollen (i.e. pollination) should be noted:

A. Enhalus

Enhalus acoroides is an obligate surface-pollinated plant with a pollination mechanism that is surprisingly similar to its freshwater relative, *Vallisneria* (Svedelius, 1904; Sculthorpe, 1967). In this case, male flowers detach underwater and float to the water surface when they are free floating and encounter the female inflorescence that remains attached to the submerged plant via a long spiral peduncle. Following pollination, in which pollen are transferred in a dry state from anther to stigma, the infructescence develops underwater. A recent study by Rollón et al. (2003) found that the length of exposure of the female inflorescence at the water surface was critical for pollination and subsequent seed set, which was higher at shallow sites.

B. Thalassia

Male flowers were found to be more numerous than females in populations of *Thalassia hemprichii* (Ehrenberg) (Pascasio and Santos, 1930). Flower development and pollination was coincident with the tidal cycles, and flowering/pollination occurred near the spring tides when the greatest water circulation was experienced (Pettitt, 1980). In this case, anthesis from submerged plants involved the release of a “coherent mass of pollen and thecal slime” (Pettitt, 1980), but no reports of pollen transport and capture have been reported. Presumably, pollen released in the canopy is transported a limited distance and can experience increased velocity near the bottom of the canopy below the area of maximal leaf area (see Okubo et al., 2002), where pollination can occur when the pollen encounter stigmas. Saltational movements involving near-bed shear are also possible due to the interaction of the elongate chains of pollen with the flow in the benthic boundary layer, although this mechanism has yet to be demonstrated.

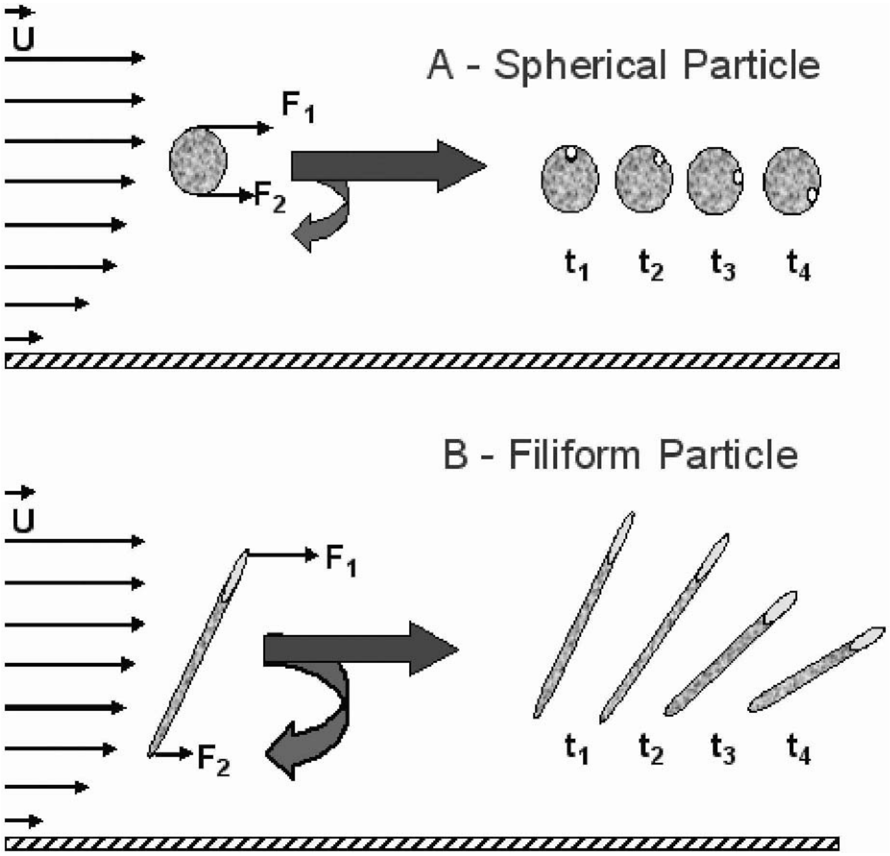

Fig. 5. The advantage of filiform pollen morphologies in seagrasses is revealed when they are compared to spherical pollen shapes. Under flowing conditions, a particle's motion is due to fluid translation, fluid rotation, and fluid deformation. Velocity gradients (boundary layers) exist around flowers and inflorescences as indicated by the velocity (U) vectors to the left. The shear in these velocity gradients cause particles to rotate as they are transported downstream in time (i.e. t_n), however the rotation is greater for filiform particles due to the larger axial force that they experience. Pollen capture can thus occur via direct interception within a streamline, rotation of pollen within $\frac{1}{2}$ a pollen length of the stigma, or via redirection in the boundary layer around inflorescences and flowers (Ackerman, 1995). Note that this figure represents a two-dimensional representation of a complex three-dimensional process (after Ackerman, 1995).

C. Halophila

Halophila has both monoecious and dioecious species (Table 2), which in the case of *Halophila beccarii* Ascherson are protogynous with mature female flowers occurring while anthers are still immature (Parthasarathy et al., 1988), and protandrous in the case of *Halophila decipiens* Ostenfeld (McMillan, 1989). The pedicel of the male flowers extends considerably before anthesis when pollen were released singly or on mass, sometimes at night (Parthasarathy et al., 1988). Following elongation of the pedicel, pollen release in *Halophila engelmannii* Ascherson involved gas bubbles that were released during anthesis under light conditions in the laboratory, which provided buoyancy for some of the pollen to rise to the water surface (McMillan and Jewett-Smith, 1988). It is important to note that no such floatation was found during the anthesis of anthers of *Halophila hawaiiana* Doty & Stone (Herbert, 1986). In this case, it is likely that pollen can be transported near the bottom of the canopy where pollen capture can occur on the long stigmatic surfaces. Interactions of the elongate pollinium with the flow around flowers near the bottom of the canopy are also anticipated (see description for *Thalassia*).

D. Amphibolis

The flowers are exposed on the ends of short branches sheltered by leaves. The anthers shed the thread-like pollen that float in the water until it contacts the slender stigmas where fertilization takes place (Black, 1913). It is also possible for some inflorescences and anthers to detach and float to the surface where they release pollen, which disperse downward through the water column (Ducker et al., 1978; McConchie and Knox, 1989b). More recent direct observations of pollination in the field indicates that male plants mature earlier than female plants with anthers shedding pollen while still attached to the plant (Verduin, 1996; Verduin et al., 1996). Pollen remained in the water column (it did not float to the surface) and pollination was assumed to be three-dimensional in which interfloral distances were on the order of 20–500 cm (Verduin et al., 1996) leading to pollination success of ∼67% based on scanning electron microscope examination of pollen on stigmas (Verduin, 1996).

E. Cymodocea

Cymodocea nodosa (Ucria) Ascherson was found to flower in equal sex ratios, but the density of flowers was clumped in distribution on small-spatial scales and tended to increase in deeper locations away from the coast (Buia and Mazella, 1991). No information is available regarding pollen transport and capture, but presumably it involves within and below canopy flow and interactions of filiform pollen with the local flow environment around female shoots and stigmas (e.g. Okubo et al., 2002).

F. Halodule

Immature anthers are white and exist within the foliage leaf; they change to green (red and cream have also been reported) on maturation with the growth of the filament that extends the anther above the leaf axil (Johnson and Williams, 1982). No information is available regarding pollen transport and capture, but presumably it involves within and below canopy flow and interactions of filiform pollen with the local flow environment around female shoots and stigmas (e.g. Okubo et al., 2002).

G. Syringodium

Immature anthers are green and extend above the floral bracts on a filament once they mature (Johnson and Williams, 1982). No information is available regarding pollen transport and capture, but presumably it involves within the canopy flow through the interactions of filiform pollen with the local flow environment around female inflorescences (e.g. Okubo et al., 2002). Laboratory studies involving flow visualization of female inflorescences of *Syringodium filiforme* Kützing in a flow chamber (Ackerman, unpublished) indicate that bracts redirect flow and generate zones of recirculation immediately downstream at moderate velocities (Fig. 4A). In wind-pollinated plants, these recirculation zones provide opportunities for pollen to be captured on the downstream side of stigmas if they have not intercepted or impacted on the upstream side of stigmas (Niklas, 1992). Whether this occurs in *Syringodium* and other seagrasses remains to be determined, especially since the response of filiform particles in downstream recirculation zones is not known.

H. Thalassodendron

There was an equal sex ratio in *Thalassodendron pachyrhizum* den Hartog, but only ∼10% of shoots in the population possessed inflorescences at any time, and further examination indicated that inflorescences were produced every 3–4 years (Kuo and Kirkman, 1987). The male inflorescences of *Thalassodendron ciliatum* (Forsskål) are bright red and consist of two flowers that mature at different times and extend on a filament at maturity (Ducker et al., 1978). Flowering in submerged *T. ciliatum* beds was also variable in space and time leading to variability in the occurrence of seedlings (Kamermans et al., 2001). Pollen dehiscence occurs on the plant or immediately after anthers detach (Kuo and Kirkman, 1987), and presumably pollen transport and capture involves within and below canopy flow and the interaction of filiform pollen with the local flow environment around female shoots and extended stigmas (e.g. Okubo et al., 2002).

I. Posidonia

There can be significant differences among sympatric *Posidonia* species in terms of the positioning of flowers (e.g. at the top of the canopy vs. within the canopy), canopy structure (e.g. random vs. row-like arrangements) and the phenology (e.g. length and duration of flowering), which probably ensure outcrossing and limit self pollination (Smith and

Walker, 2002). The plants appear to be protandrous with pollen release preceding stigma receptivity (Smith and Walker, 2002). Cavolini (1792 translated in König, 1805) suggested that some of the large amounts of cotton-like pollen must contact stigmas. Indeed, dye release studies and pollen capture experiments in the field indicated that pollen dispersal distances were greater for *Posidonia australis* Hooker f. (flowers at the top of canopy) than *Posidonia sinuosa* (flowers within the canopy), and that these differences were reflected in the degree of genetic variability of the two species (Smith, 2000).

J. Heterozostera

Sexual reproduction in *Heterozostera tasmanica* (Martens *ex* Ascherson) den Hartog (Campey et al., 2002) was variable in time and space and was not evident in some years. The maximum seed production was <20% over 3 years, but some seeds may have been exported from the system by hydrodynamic processes or eaten by predators. It is likely that pollen transport and capture is similar to that of *Nanozostera* and *Zostera* given the similarities in the inflorescence and floral structures (see below). Note that Les et al. (2002) and Waycott et al. (Chapter 2) collapse *Heterzostera* into *Zostera*.

K. Phyllospadix

There is considerable spatial variation in the location of male and female clones and female clones were more common than males in the upper intertidal (Williams, 1995). Field observations indicate that anthers exposed to air dehisce pollen on the water surface and pollinate stigmas of exposed female plants, however pollen was also released underwater during ebb tide when they pollinate submerged stigmas (Dudley, 1893). Additional information on the nature of pollination in the exposed rocky intertidal zone is needed.

L. Zostera and Nanozostera

Zostera marina is the best characterized seagrass species in terms of the mechanics of pollination, and Clavaud (1878) noted that water motion carried the pollen. Pollen transport and capture was characterized in a laboratory flow chamber using stroboscopic photography and in the field using pollen models and gel-coated surfaces (Ackerman, 1997a,b, 2002). In the lab, pollination was found to occur under smooth and viscous conditions (lower Reynolds number) rather than the turbulent eddies described for wind pollination (Fig. 4B; see Niklas, 1992; Ackerman, 2000). Morphological changes during phenology, namely the emergence of female flowers, led to an increase in the fluid shear stress around the inflorescence (Ackerman, 1997a). Filamentous pollen (2,700 × 7.5 μm) rotated and crossed streamlines towards female flowers in the flow (Fig. 5; Ackerman, 1997b) due to an axial force that is directly related to the length and aspect ratio of the pollen (Forgacs and Mason, 1958). In contrast to spherical pollen, pollination occurs through one of three mechanisms: (1) direct interception on stigmas; (2) rotation within $^1/_2$ a pollen length of stigmas; and (3) by being redirected through streamlines towards carpellate flowers (Ackerman, 1997b). Field measurements revealed that flow within the canopy at the scale of inflorescences and flowers was similar to those used in the laboratory (Ackerman and Okubo, 1993), and the differential capture of filamentous vs. spherical particles in the canopy support these aforementioned pollen and transport mechanisms (Ackerman, 2002). Importantly, it was estimated that between 10^3 and 10^4 *Z. marina* pollen are required to pollinate a single flower, an estimate which is similar to the measured pollen–ovule ratio in this species (Ackerman, 1993; see below).

VIII. Post-Pollination: Pollen Tubes, Embryonic and Seedling Development

As in other angiosperms, following the transfer of pollen to stigma, the pollen germinates and a pollen tube grows through the stigma, style, and locule to the micropyle of the ovule where it penetrates the synergid cells (e.g. Raven et al., 1999; Kuo and den Hartog, Chapter 3). The pollen tube facilitates the transfer of sperm cells that fertilize the egg cell and the endosperm nucleus. As indicated above, post-pollination processes are complicated in seagrasses by the complete submergence of reproductive organs in the marine environment (McConchie and Knox, 1989a). Consequently, pollen and stigmas have a waterproof adhesive that

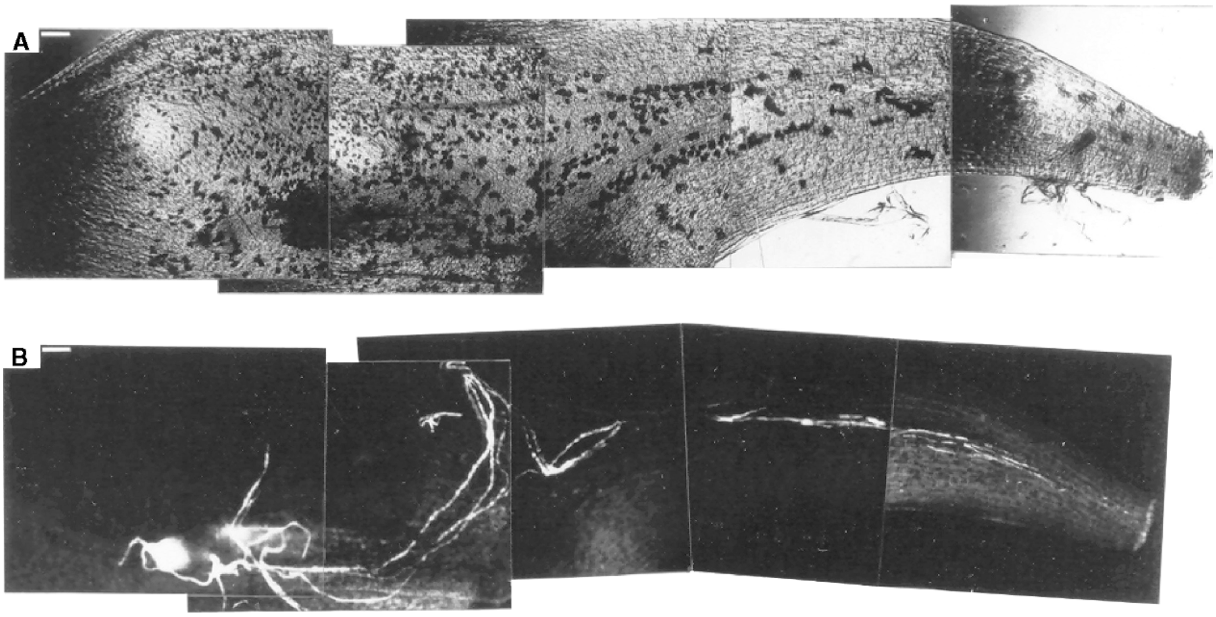

Fig. 6. Pollen tube growth in the *Zostera marina* under (A) bright field and (B) epifluorescence using alanine blue dye. This composite representation includes images from the style at right (note the abscission scar, where the stigmas were lost) to the rear of the locule at left. Note the location of the uniovulate ovary in the second left-most image and the penetration of the egg apparatus indicated by the bright fluorescence near the micropyle (scale bar = 100 μm; modified from Ackerman, 1993).

operates on contact and serves to maintain the contact between pollen and stigma for some time (Pettitt, 1984). It is relevant to note that pollen longevity is on the order of a day in *Zostera* and *Posidonia* (de Cock, 1980; Smith and Walker, 2002). This is important as pollen germination requires several hours of contact with stigmas (Ackerman, 1993). This may appear to contradict reports of precocious pollen germination (e.g. Clavaud, 1878), but germination appears to require the presence of stigma-borne chemicals ("stigmatic" or "germination" factors) in the water or growth medium (de Cock, 1978; McConchie and Knox, 1989b). Pollen germination is evident as protuberances or beads on the filiform pollen (Hofmeister, 1852) that eventually grow between the swollen stigmatic cells (Clavaud, 1878; McConchie and Knox, 1989b; Ackerman, 1993) into the carpellate flower. In the case of *Z. marina,* pollen growth was continuous through the style, but lacked orientation at the entrance of the locule (second-third image of Fig. 6) and then again near the rear of the locule opposite the ovary (not shown). This lack of orientation and the observation of multiple pollen tubes within a single carpel speak to the possibility of pollen-tube competition and potential of an incompatibility system in seagrasses (Ackerman, 1993; c.f. McConchie and Knox, 1989b). Regardless, the time required for pollen tubes to reach the ovary was between 7 and 11 h in *Z. marina* (Hofmeister, 1852; Johansen, 1940; Ackerman, 1993).

The embryonic and seedling development of seagrasses is also an area of interest. Mature seeds lack endosperm, which is resorbed as the embryo matures (Table 2; Tomlinson, 1982). The endosperm develops via helobian endosperm development in the Hydrocharitaceae and via nuclear endosperm development in the Zosteraceae, which reinforces the concept of polyphylly of the seagrasses (Tomlinson, 1982). Embryonic development leads to an enlarged hypocotyl, which may be straight in *Thalassia* and curved in *Zostera* (Tomlinson, 1982). These features may serve to orient and stabilize the plants in the sediments (Cook, 1987). Seedling development has been best described in *Z. marina* (Hofmeister, 1852; Rosenberg, 1901b; Taylor, 1957a,b; Churchill, 1983), although data exist for *Enhalus* (Kausik, 1940), *Cymodocea* (Bornet, 1864), *Halophila* (Balfour, 1879; ecological characteristics in Zakaria et al., 1999), and *Posidonia* (Balestri et al., 1998), and it is an area of renewed research as it relates directly to the recruitment of new individuals to a population.

As in other aquatic plants the dispersal of seagrass diaspores (fruit, seed) is not well described (Van der Pijl, 1972; Hay et al., 2000), even though the Greek Botanist Theophrastus noted the occurrence of the "sea oak", which was the free-floating fruit of *Posidonia oceanica* (L.) Delile (Cavolini, 1792 translated by König, 1805). Fortunately, the recognition of the importance and relevance of seagrass diaspore dispersal phenomena has received more attention of late (Orth et al., Chapter 5). There is a great deal of diversity in the morphology and dispersal ecology of seagrass diaspores although a number of patterns are evident (Table 2). For example, seven seagrass genera have dormant seeds, and *Halodule*, *Cymodocea*, and *Halophila* release their seeds at or under the sediment (geocarpy), which may facilitate recovery from disturbances in *Halodule* (Table 2; Inglis, 2000). At least two genera (*Amphibolis* and *Thalassodendron*) have viviparous seedlings that germinate on the female plant and disperse following their detachment at a larger size, much like mangroves (den Hartog, 1970; Fig. 15, Chapter 3). Interestingly, *Amphibolis* has a comb-like orientation and grappling device on the seedling that apparently aids in seedling establishment (den Hartog, 1970). Vivipary and vegetative propagation of reproductive shoots has also been noted in other genera (*Zostera* and *Heterozostera*), but this appears to be an occasional/rare event that may serve in the dispersal phase of the detached reproductive material (e.g. Addy, 1947; Cambridge et al., 1983). A number of genera (*Phyllospadix* and *Zostera*) release relatively small, negatively buoyant diaspores that would likely disperse $\sim$1–10 ($<$100) m horizontally under normal conditions (Okubo et al., 2002). It is interesting to note that the bifid, barbed fruits of *Phyllospadix* require regions with branched turf forming algae (with cylindrical thalli) onto which they recruit (Turner, 1983). However, as indicated above for *Z. marina*, there are opportunities for detached fruiting material to disperse over great distances (see below) and for seeds to float on bubbles, which can extend dispersal distances to $\sim$10–100 m (Churchill et al., 1985). Floatation of buoyant diaspores (*Enhalus, Thalassia,* and *Posidonia*) and detached infructescences and reproductive material extend dispersal distance to $\sim$100 m–10 km (e.g. Harwell and Orth, 2002; Lacap et al., 2002; Orth et al., Chapter 5). It has long been speculated that animal mediated dispersal in the guts of birds, sea turtles, and fish could lead to very large dispersal distances to $\sim$100 m–1000 km, especially in migrating birds (e.g. Baldwin and Lovvorn, 1994).

IX. Evidence for Pollination Success

There are a number of ways in which to ascertain the level of pollination success in seagrasses including morphological analysis, phenological observation, field observation of fruiting and seedling establishment, and population genetics inferred from allozyme variation and molecular analysis. The determination of the pollen to ovule ratios has been used to estimate the relative contribution of pollen to ovules and thus establish the efficiency of pollination syndromes (e.g. Faegri and van der Pijl, 1979). Unfortunately, this approach led to the incorrect conclusion that wind pollination is a wasteful process because of high pollen–ovule ratios (i.e. $>10^6$:1). These high rates are likely a function of metabolic costs and/or intermale competition and consequently can be equally high in insect pollinated plants (see Ackerman, 2000). Regardless, this approach has been applied to a limited number of seagrasses and freshwater plants. Pollen–ovule ratios in seagrasses range from 10:1 in *Enhalus*, to 10^4:1 in *Zostera, Phyllospadix*, and *Amphibolis*, and 10^5:1 in *Posidonia* (Kausik, 1941; Ackerman, 1993; Williams, 1995; Verduin et al., 2000; Smith and Walker, 2002). Whereas the variability appears rather large, it should be recalled that *Enhalus* is an obligate ephydrophilous plant, and wide variation has also been noted in hydrophilous freshwater plants (e.g. 10^2:1 to 10^4:1; Philbrick and Anderson, 1987; Huang et al., 2001). Given this variation and the limitations of this approach, it is difficult to draw any clear conclusions about the pollen–ovule ratios in seagrasses.

Field observations of phenology, proportion of reproductive activity, seedling recruitment and outcrossing (Waycott et al., Chapter 2) provide necessary information to support the importance of successful sexual reproduction. This is especially true in the aforementioned annual populations that must recruit each year from seed banks due to excessive heat or ice scouring (e.g. Keddy and Patriquin, 1978; Meling-Lopez and Ibarra-Obando, 1999). The number and diversity of local studies of phenology of individual species are too numerous to include here, but Rollón et al. (2003) provide an excellent example in the case of *Enhalus acoroides*. The relevant information from these studies is that sexual reproduction may or may not be of local importance. A recent study, however, revealed that developmental and ecological interaction (e.g. abortion and seed predation) can have significant effects on fruit and seed production, which could be interpreted as failures in pollination success in the absence of careful longitudinal study (Balestri and Cinelli, 2003). This is clearly a topic that should be examined in more detail.

There is considerable evidence from enzyme and genetic analysis that sexual reproduction is important for local gene flow (Waycott et al., Chapter 2). For example, this appears to be the case in *Thalassia* for local gene flow but not for exchanges over km scales (Schlueter and Guttman, 1998). Molecular analyses reveal high outcrossing rates in *Zostera* and *Posidonia* (Ruckleshaus, 1995; Waycott and Sampson, 1997; Reusch, 2000), but not for example in *Amphibolis* (Waycott et al., 1996). It is interesting to note that previous reports of genetic uniformity in some seagrasses have proven false with the application of different or new techniques (see review in Reusch, 2001). From the perspective of this contribution, it is satisfying to note that outcrossing rates in *Posidonia australis* were higher in energetic environments where pollen transfer would be enhanced, and that these rates were more similar to those of entomophilous plants than anemophilous ones (Waycott and Sampson, 1997). Clearly, additional research in this area is needed, especially studies that integrate the examination of pollen transport phenomena with genetic analysis.

X. Conclusions

The reproductive biology of the 12–13 genera of seagrasses is reviewed from a morphological, ecological, and functional perspective. Seagrasses are an artificial grouping of unrelated monocotyledonous plants that have successfully invaded the marine coastal environment. Whereas much of their reproductive biology resembles that of their freshwater relatives, there are a number of characteristics that are unique and which have evolved independently within the various lineages. Generally, seagrasses have drab, highly reduced flowers, and exhibit dioecy (9 genera) and dichogamy (4 genera), all characteristics of abiotically and submarine pollinated plants. The floral structures are either axillary near the seafloor, or borne on reproductive shoots within or near the top of the canopy; one genus has a pedunculate female inflorescence and free-floating male flowers. Carpellate reproductive structures are generally elongated bifid stigmas, although unbranched, thrice-branched, and disc-shaped stigmas are also present. Staminate structures are generally simple anther sacs in which filiform or functionally filiform pollen, which have evolved convergently and functionally, are housed. Anthesis generally occurs following the elongation of a simple filament and water currents are required to disperse pollen, which is released under water from detached anthers or in some cases on the water surface from free-floating male flowers or exposed plants. Pollination appears to be mediated by fluid–dynamic interactions between the filiform pollen and the velocity gradients around carpellate flowers, which lead to rotational movements and repositioning in the flow as pollen is transported around flowers. This biomechanical response of filiform pollen increases the opportunity for pollination and thus represents a selective advantage for these submarine pollinated plants.

It is evident that the patterns of sexual reproduction in seagrasses are becoming better understood, especially with respect to morphology and phenology, although much of the data exist for a few model species. For example, it is possible to map the particular pollen morphology onto the general phylogeny of seagrasses and come to some reasonable conclusions about the convergent evolution of this group. Much information, however, is lacking; for example, morphological measurements of pollen length remain to be reported in most species and indeed some genera (see Table 2). Notwithstanding this progress, there is an almost complete lack of understanding of the pollination process in most seagrass genera (see above) and much of the descriptive information is from the 19th century! Again, we have what amounts to a reasonable understanding of the physical ecology of pollination in *Zostera marina* and a glimpse of what occurs in *Amphibolis antarctica* (Labille) Sonder et Ascherson, several Australian *Posidonia* species, and *Syringodium filiforme*. Whereas this does not establish a paradigm in the true sense, it does provide a biomechanical model that can be examined rigorously in the laboratory and the field. More importantly, this realization provides considerable opportunities for exciting research in coastal ecosystems throughout the globe.

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Chapter 5

Ecology of Seagrass Seeds and Seagrass Dispersal Processes

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I. Introduction

Seagrasses began colonizing the marine environment 100 million years ago in the Cretaceaous (den Hartog, 1970) and, like their terrestrial, wetland, and freshwater angiosperm counterparts, established a highly effective method of dispersal - seeds. While the terrestrial plant literature is replete with studies on all aspects of seed ecology, ranging from the importance of seed size and storage reserves, morphology, to dispersal and recruitment strategies (see reviews by Baskin and Baskin, 1998; Clark et al., 1998; Nathan and Muller-Landau, 2000; Higgins et al., 2003; Levin et al., 2003) research on the ecology of seagrass seeds has been remarkably sparse. These processes are integral to understanding the demography of natural plant populations and the absence of this information for seagrasses led to the historical paradigm that seeds were unimportant in seagrass bed dynamics. However, recent studies demonstrating higher than expected genetic diversity (Waycott, 1995; Reusch, 2002), patch development due to seed recruitment (Duarte and Sand-Jensen, 1990; Olesen and Sand-Jensen, 1994; Frederiksen et al., 2004; Meehan and West, 2004; Olesen et al., 2004; Duarte et al., Chapter 11), and more rapid recovery of disturbed stands than expected from vegetative propagation alone (Preen et al., 1995; Cambridge et al., 2002; Plus et al., 2003; Whitfield et al., 2004; Greve et al., 2005) have focused attention to seeds, seed production and the fate of seeds, dispersal and recruitment strategies, and the potential role of seeds in seagrass restoration projects (Williams and Davis, 1996; Harwell and Orth, 1999; Kenworthy, 2000; Orth et al., 2000; Inglis, 2000a; Orth et al., 2003; Balestri and Bertini, 2003; van Katwijk and Wijgergangs, 2004).

The objectives of this chapter are:

1. To review basic aspects of what is known about seeds and the seed ecology of seagrasses, in particular processes important in their dispersal and recruitment,
2. to provide the conceptual basis for emerging paradigms in this field, and
3. to highlight the relevance of sexual propagules for the restoration and conservation of seagrass meadows.

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Table 1. Dispersal and dormancy characteristics of the sexual diaspores (defined as the plant propagule that is most easily dispersed) of the twelve seagrass genera which are grouped according to the phylogenetic classification of Les et al. (1997) (Cymodoceae—*Halodule*, *Cymodocea*, *Syringodium*, *Amphibolis*, *Thalassodendron*; Zosteraceae—*Phyllospadix*, *Zostera*, *Heterozostera*; Hydrocharitaceae—*Enhalus*, *Thalassia*, *Halophila*; Posidoniaceae—*Posidonia*).

Genus	Diaspore	Seeds per fruit	Fruit/ Seedsize (mm)	Position of release	Buoyancy potential	Seed bank dormancy	Max. seed density (m^{-2})	Max. % germinated seeds	Seedling survival (%)	Reference[c]
Halodule	Fruit	1	2–3	Sub-surface	Poor	Persistent	20,000	2	<2	1,2,3,4,5,6,7, 19,35,38
Cymodocea	Fruit	1	7–10	Sub-surface	Poor	Persistent	1,300	2–5	10–20	1,7,8,9,10,17, 25,26,31
Syringodium	Fruit	1	4–8	Elevated	Poor	Persistent	9,500	7	nd	1,4,6,7,17, 38,56
Amphibolis	Seedling	1	80–100[a]	Elevated	Good	Viviparous	nd	nd	nd	1,17
Thalassodendron	Seedling	1	35–50[a]	Elevated	Good	Viviparous	nd	nd	nd	1,17
Phyllospadix	Reproductive Shoot/ rhipidia/ spathe[b]	1	9–11	Elevated	Moderate	Transient	11,700	90	0–10	1,17,22,41,42, 43,44,53
Zostera	Reproductive Shoot/ rhipidia/ spathe[b]	1	2–4	Elevated	Good/ Moderate	Transient	9,000	50–90	0–40	1,7,11,12,13, 14,15,16,17, 18,20,21,24, 27,28,45,48, 50,55,57,58
Heterozostera	Reproductive Shoot/ rhipidia/ spathe[b]	1	3–4	Elevated	Good/ Moderate	Transient	nd	nd	nd	1,17
Enhalus	Fruit/seed	8–14	10–15	Elevated	Good	Indistinct	nd	nd	nd	1,17,54
Thalassia	Fruit/seed	3–9	8–10	Sediment surface	Good	Indistinct	230	nd	11	1,17,23, 51,52,54
Halophila	Fruit/seed	7–60	0.2–1	Sub-surface/ Elevated	Moderate/ Poor	Transient/ Persistent	70,000	12–63	nd	1,17,30,32, 33,34,35,36, 37,40,47,49
Posidonia	Fruit/pedicel	1	8–20	Elevated	Good	Indistinct	450	50–90	0–67	1,10,17,39, 46,49

nd = no data

Estimates of the maximum recorded densities of seeds, proportion of the seedbank that germinated in-situ and seedling survival were obtained from published literature ([a] these two genera produce viviparous young which grow for some period on the parent. Size given here is the dispersing seedling; [b] these genera have a reproductive shoot that can dislodge entirely, or in parts such as the rhipidia or individual spathes, and float) (revised from Inglis, 2000) (reprinted with the permission of Pacific Conservation Biology). [c]1 = den Hartog (1970), 2 = Bragg and McMillan (1986), 3 = Inglis (unpublished data), 4 = McMillan (1981), 5 = McMillan (1983), 6 = McMillan (1991), 7 = Clarke and Kirkman (1989), 8 = Terrados (1993), 9 = Caye and Meinesz (1986), 10 = Buia and Mazzella (1991), 11 = Harrison (1993), 12 = Hootsman et al. (1987), 13 = van Lent and Verschuure (1994), 14 = Phillips et al. (1983), 15 = Conacher et al. (1994a), 16 = Conacher et al. (1994b), 17 = McConchie and Knox (1989), 18 = Kirkman et al. (1982), 19 = Ferguson et al. (1993), 20 = van Lent and Verschuure (1995), 21 = Orth et al. (1994), 22 = Kuo et al. (1990), 23 = Lewis and Phillips (1980), 24 = Moore et al. (1993), 25 = McMillan et al. (1982), 26 = Caye and Meinesz (1985), 27 = Churchill (1983), 28 = de Cock (1980), 29 = McMillan (1982), 30 = Kuo et al. (1993), 31 = Reyes et al. (1995), 32 = Jewett-Smith and McMillan (1990), 33 = McMillan and Jewett-Smith (1988), 34 = Kuo and Kirkman (1992), 35 = McMillan (1976), 36 = McMillan (1987), 37 = Birch (1981), 38 = Johnson and Williams (1982), 39 = Waycott (1995), 40 = McMillan (1988a,b), 41 = Williams (1995), 42 = Turner (1983), 43 = Turner (1985), 44 = Turner and Lucas (1985), 45 = Peterken and Conacher (1997), 46 = Balestri et al. (1998), 47 = McMillan and Soong (1989), 48 = Brenchley and Probert (1998), 49 = Kirkman (1998), 50 = Wyllie-Echeverria et al. (2003), 51 = Kaldy and Dunton (1999), 52 = Kaldy and Dunton (2000), 53 = Blanchette et al. (1999), 54 = Lacap et al. (2002), 55 = Harwell and Orth (2002a), 56 = Peterson et al. (2002), 57 = Orth et al. (2003), 58 = Olesen (1999).

II. Seeds and Seed Production

Seed size, anatomy and germination dynamics differ dramatically among seagrass species (den Hartog, 1970; Orth et al., 2000; Inglis, 2000a) (Table 1). Kuo and Kirkman (1996) categorized the seagrass genera into three groupings based on seed anatomy and germination history:

1. Species with seeds that have a fleshy or membranous seed coat and no distinct dormancy period (e.g. *Enhalus*, *Posidonia* spp., *Thalassia* spp.),
2. species with seeds with a hard seed coat and distinct dormancy period (e.g. *Zostera* spp., *Halophila* spp.), and
3. species with seeds that do not have a seed coat, no distinct dormancy period, and where seedlings develop for some time period on the parent plant (e.g. *Amphibolis* spp., *Thalassodendron* spp.).

Seagrasses have evolved a variety of reproductive strategies (dioecy, monoecy, and hermaphroditism) and functional morphologies to insure successful pollination in an aquatic environment (Cox, 1988; Ackerman, 1995, 1997a,b; 2000; Ackerman, Chapter 4, this volume). Bottlenecks for successful pollination are expected to be more prominent in dioecious species (over 60% of seagrass species are dioecious) where rarity of either sex could lead to the reduction or absence of pollen or flowers, or in species where pollen dispersal occurs over short distances (Cox, 1988; Ruckelhaus, 1996), although recent research challenges the latter (Ackerman, 2002). Seed production would obviously be problematic where meadows are entirely dominated by one sex, or in beds with asynchronous flowering (Caye and Meinesz, 1985; Buia and Mazzella, 1991; Terrados, 1993). However, in the only study to examine the influence of unequal sex ratios on seed production, Williams (1995) showed that, despite the rarity of male flowers in a sub-tidal population of *Phyllospadix torreyi*, almost all ovules had been fertilized, most likely facilitated by the strong mixing characteristics of the surrounding environment.

Seagrass seed size varies by two orders of magnitude among species, ranging from 0.2 mm in *Halophila* to 20 mm in *Posidonia*. Most seagrass genera produce only one seed per fruit, but some, such as *Halophila*, set up to 60 seeds per fruit, although there is some variation within particular genera for both seed size and the number of seeds per fruit (Table 1). Moles and Westoby (2003) showed a ten-fold reduction in mean seed mass of terrestrial plants for every 23° increase in latitude (they did show a wide range of seed mass within a latitude), possibly due to habitat type, plant growth form, seed disperser assemblage, length of the growing period, or net primary productivity. Comparable information for seagrass species is sparse (Wyllie-Echeverria et al., 2003).

Seagrass seed production (densities m^{-2}) vary by more than two orders of magnitude among the various genera (Table 1) with the largest number produced by those species that have relatively hard seed coats and some period of dormancy. In terrestrial plants, significant variation in seed production occurs in space and time (e.g. masting), so that seed production in some places and years contribute to more long-term population success than others. Similarly, large interannual (Orth and Moore, 1986; Inglis and Lincoln Smith, 1998) and spatial (Inglis and Lincoln Smith, 1998; Inglis, 2000b) fluctuations have been recorded in the reproductive output of seagrasses, but the relationship between seed production and seedling recruitment is unclear.

III. Seed Banks, Dormancy, and Seed Germination

Published estimates of sediment seed bank densities in seagrass communities are generally comparable to those of most plant community types (Fenner, 1995; Orth et al., 2000). Like seed banks in terrestrial systems, they are highly variable both in space and time and may bear little or no relationship to the spatial distribution of plants that produce the seeds. Harrison (1993) documented the spatial and temporal dynamics of a *Zostera marina* seed bank in The Netherlands, showing high variability in a single population. A significant portion of the seeds in the seed bank was lost to natural mortality and a small percentage of the seeds contributed to a persistent seed bank. Inglis (2000b) found significant heterogeneity in *Halodule uninervis* seed banks at multiple spatial scales and reported “no obvious spatial relationships between densities of flowering shoots, vegetative shoots, developing ovules, and seed bank densities that might indicate consistent patches of seed production and storage.” Harwell and Orth (2002b) also found extreme variability in *Z. marina* seed banks similar to those of Inglis (2000b). Future studies of seagrass seed banks must recognize the dynamic nature of a seed bank and that the vagaries of currents, storm events, waves, and bottom structure probably determine more about the location and density of seed deposition than do floral characteristics, i.e. flowering shoot density (Inglis, 2000b; Inglis and Waycott, 2001).

Seed banks are often classified as transient (turnover in less than one year) or persistent (remaining viable longer than one year) according to how long seeds remain viable in the sediment. Persistence of a seed in the seed bank will depend, in part, on whether the species in question has evolved some mechanism for its seed to remain dormant within the sediment. Dormancy is generally classified according to the residence time in the sediment, the timing of initiation of dormancy (e.g. during seed development or seed release), or the mechanisms preventing germination (e.g. environmental, physical or physiological; Baskin and Baskin, 1998). Several seagrass genera, notably *Posidonia*, *Thalassia*, and *Amphibolis*, produce seeds that are already germinating within the fruit and thus have no dormancy period or seed bank (e.g. see Rollon et al., 2003). The remaining genera produce seeds that can remain dormant from weeks to months or years. McMillan (1991) showed that seeds of a variety of species are capable of surviving longer than 12 months under laboratory conditions: *Syringodium filiforme*—49 months; *H. uninervis*—41 months; *Halophila engelmannii*—24 months; *Halodule wrightii*—up to 46 months. Whether these estimates of dormancy also apply to seeds in natural field settings remains a topic for future research. An important question that must be resolved is whether dormancy is maintained by environmental control, seed coat inhibition, physiological characteristics of the seed, or some combination of all three influences (Baskin and Baskin, 1998; Orth et al., 2000).

Salinity, temperature, light, scarification of the seed coat, and oxygen (oxygen-reduction profiles or E_h) have been shown to be critical cues influencing seagrass seed germination from field and laboratory studies. Of these, salinity has generally been thought to be the most influential factor (see review in Orth et al., 2000). Nevertheless, there are significant questions about whether the changes in temperature and salinity that have been shown to initiate germination in the laboratory are actually experienced by seeds in the sediment, where the interstitial water is relatively poorly flushed. Moreover, most studies have not separated the confounding influences of osmotic shock and seed coat removal (often a consequence of osmotic shock) in initiating germination. Temperature stratification, photoperiod, and specific wavelengths of light are important cues for the germination of terrestrial plants (Baskin and Baskin, 1998) and freshwater submersed aquatic vegetation (e.g. Choudhuri, 1966; Ferasol et al., 1995; Kimber et al., 1995) but their influence on the germination of seagrass seeds has not been studied. Recent studies of germination by *Z. marina* seeds suggest that reducing conditions, which occur in anoxic sediments may be critical for inducing germination, in particular when coupled to temperature changes (Kawasaki, 1993; Moore et al., 1993; Brenchley and Probert, 1998; Inglis, 2000c). While ecologically meaningful studies are needed to determine proximate and ultimate causes of seed germination, it appears that sediment reducing conditions may play a crucial role in this process and should be considered in any future seed germination experiment where seeds lie dormant in sediment for some unspecified period of time.

In some terrestrial plants, seed germination also appears to be under strong genetic control, so that populations in temporally variable environments retain more polymorphic germination responses than those in more stable conditions (Meyer and Allen, 1999). In seagrasses, the importance of seed production and germination also appears to vary among populations subject to different frequencies of environmental disturbance, with observations suggesting increased flowering in areas subject to increased stress (Phillips and Backman, 1983; Harrison, 1993). This may reflect both proximate environmental cues for germination and genetic predisposition. Rhode (2002) documented strong phenotypic plasticity in the reproductive cycle of *Z. marina*. Williams (2001) has shown significant positive associations between the genetic diversity of *Z. marina* populations and the frequency and success of sexual reproduction. More seeds germinated from a genetically diverse, untransplanted population than from a transplanted population that had low genetic diversity (Williams, 2001). Similar variation in seed viability and ability to germinate may be expressed in natural populations as a result of variation in the rate of outcrossing.

IV. Seed Dispersal

All subsequent processes that influence plant population dynamics (e.g. predation and competition) are dependent on the dispersal of a seed to some suitable site, although it is possible that factors influencing seed output before they are dispersed (e.g. predation on fruit on the parent plant before seeds are mature) can be equally important (Holbrook et al., 2000). Selective forces hypothesized to produce plants adapted for seed dispersal include, allowing seeds to escape higher mortality

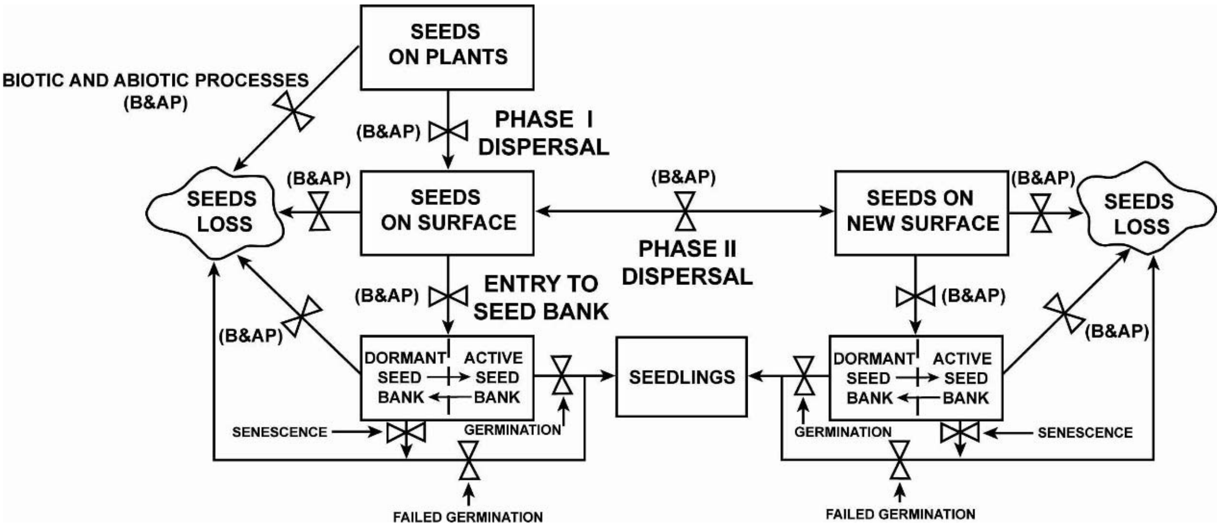

Fig. 1. Conceptual model of movement of seeds from the parent plant to its final location emphasizing two distinct but equally important dispersal stages: Phase I which is dispersal of a seed from the parent plant to an initial surface, and Phase II which is dispersal of a seed from its initial surface to a new surface to its final position. Dispersal can be either by biotic (B) and abiotic (A) processes (P) (from Chambers and MacMahon, 1994, reprinted with permission from Annual Review of Ecology and Systematics).

rates near parents (escape, or Janzen-Connell hypothesis), colonizing distant disturbed, but relatively non-competitive habitats (colonization hypothesis), or finding distinct microhabitats (directed dispersal hypothesis) (Janzen, 1970; Connell, 1971; Howe and Smallwood, 1982; Harms et al., 2000). Numerous studies in terrestrial ecology have focused on various aspects of seed dispersal ranging from dispersal distances from the parent plant, characteristics of the seed that enhances seed dispersal, seed dispersion patterns around the parent plant, and the relative influence of biotic (animal mediated) vs. abiotic (wind or water) processes in mediating dispersal (reviewed in Howe and Smallwood, 1982; Chambers and MacMahon, 1994).

Terrestrial studies on seed dispersal have concentrated on the movement of seeds from the parent plant to a particular surface (often referred to as Phase I, primary, or ‘coarse’ dispersal). However, subsequent movement of seeds from that surface to another surface (often referred to as Phase II, secondary or ‘fine’ dispersal) (Fig. 1) may also be significant. Secondary dispersal is less studied than primary dispersal yet can have important consequences for vegetation structure (Chambers and MacMahon, 1994; Nathan and Muller-Landau, 2000; Wang and Smith, 2002). One of the major issues surrounding both primary and secondary dispersal is the mechanism of how a seed is actually dispersed. While many seeds are often classified as abiotic (wind) or biotic (animal) dispersed it is likely seeds are dispersed from multiple mechanisms (Wilkinson, 1997, 1999). Higgins et al. (2003) recently argued that long distance dispersal of plants can occur frequently from non-standard mechanisms, i.e. seeds that are morphologically designed for wind dispersal can be dispersed by birds over long distances.

Seed dispersal in some seagrasses may follow the sequence outlined by Chambers and MacMahon (1994) and Nathan and Muller-Landau (2000) with Phase I or primary dispersal involving floating reproductive fragments, buoyant fruits with viable seeds, or buoyant seedlings and secondary dispersal occurring when seeds arrive at the sediment surface as ‘seed rain’ (Figs. 2 and 3). While the dispersal distance of a floating reproductive propagule can be quite large (10^3 m as noted for *Z. marina* reproductive fragments (Reusch, 2002; Harwell and Orth, 2002a), or *Enhalus* and *Thalassia* fruits (Kaldy and Dunton, 1999; Lacap et al., 2002) (Table 2), seeds on the sediment surface have dispersal distances one to two orders of magnitude less (Table 2). Seeds are negatively buoyant and settle rapidly to the sediment surface (Table 2) when released at the surface. Surface micro-topographic features such as sand ripples, animal tubes, or bioturbation structures such as sediment mounds can influence seed

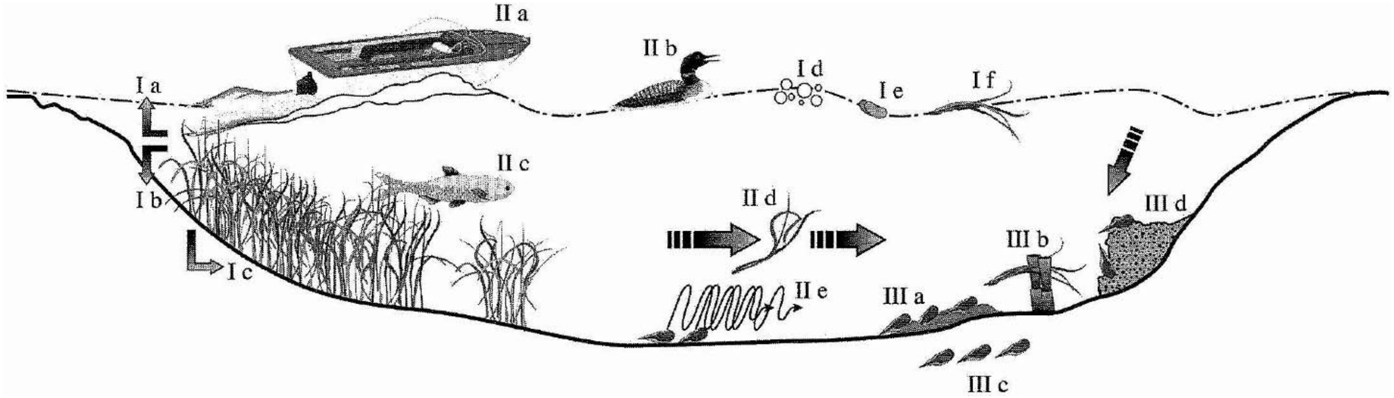

Fig. 2. Graphic showing potential avenues (following Chambers and MacMahon, 1994) of seagrass seed dispersal to a seed's final resting position. Phase I (Primary dispersal): (a) seed release to water column can also be the fruit or either the whole plant or parts (spathe or rhipidia of *Zostera*), (b) seed release onto sediment surface, c. seed release below sediment surface, d. air bubble, e. buoyant fruit (*Posidonia*, *Thalassia*), f. floating shoot or fragment (*Zostera*); Phase II (Secondary dispersal): (a) ballast, (b) waterfowl, (c) fish, (d) sub-surface water column transport of reproductive shoot or fragments or fruits, (e) bedload transport; Phase III (Final resting position): (a) seed entrained by bottom microtopographic features (e.g. sand ripples, worm castings or feeding depressions), (b) entrainment of reproductive structure into worm tubes, (c) seed (*Phyllospadix*) or seedling (*Amphibolis*) hooked onto macroalgae, (d) seed in the sediment seed bank.

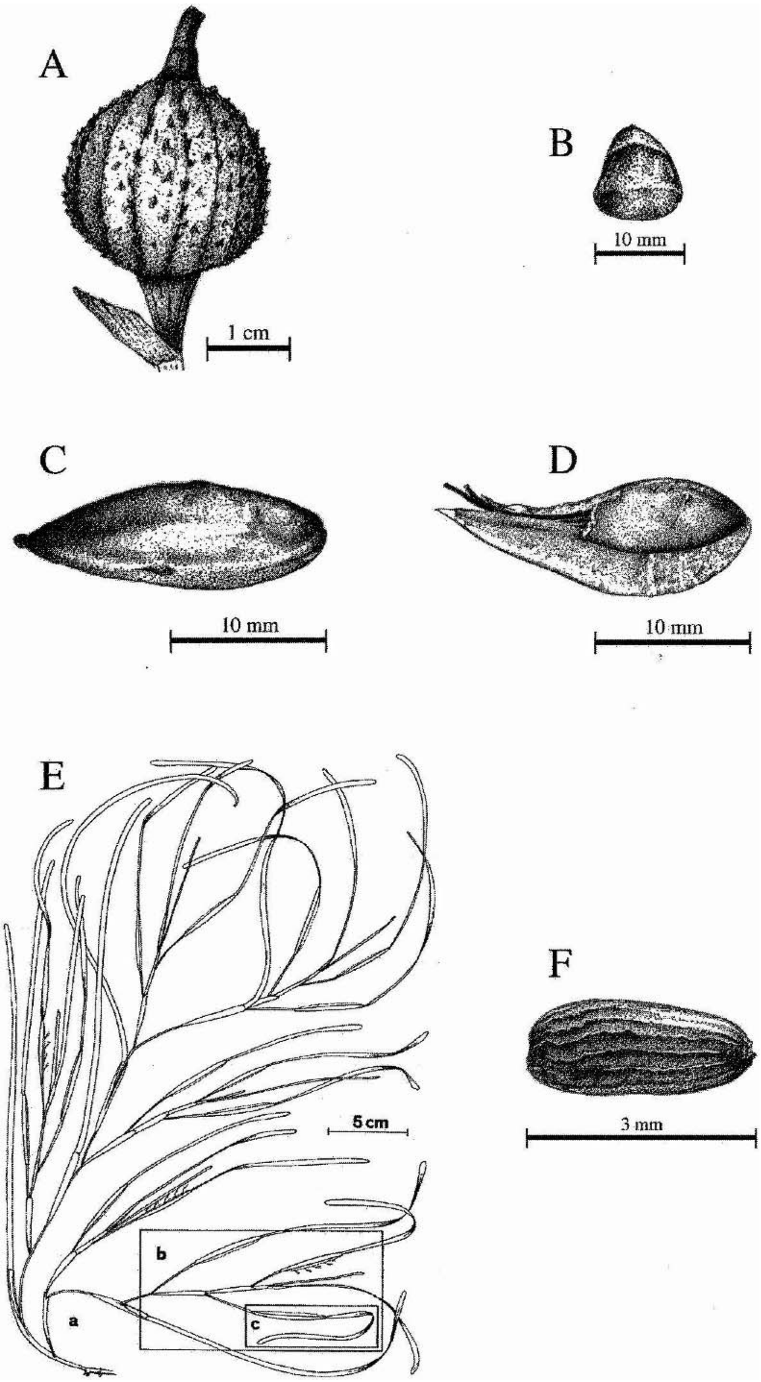

Fig. 3. Diaspores (dispersing units) for *Thalassia testudinum*, *Posidonia australis*, and *Zostera marina*. The large fleshy fruit of *Thalassia* (A) and *Posidonia* (C) and either flowering shoot (i), rhipidia (ii), or spathe (iii) of *Zostera* (E) provide for the long distance component in these species. Seeds of *Thalassia* (B) can float but for significantly shorter periods than the fruit. Seeds of *Posidonia* (D) and *Zostera* (F) do not float and will settle rapidly to the sediment surface but will not move far from where they settle under most conditions. Occasionally, a *Zostera* seed is released from the spathe with a bubble and can float several hundred meters from the parent plant (3E, reprinted with permission of Aquatic Botany (see acknowledgement section for additional information); 3A, adapted from photographs provided by J. Kenworthy and J. Kaldy).

Table 2. Dispersal distances, buoyancy, and fall velocities of seagrass propagules.

Species	Location	Dispersal unit	Buoyancy time	Fall velocity (cm s^{-1})	Distance (km)	Source
Thalassia testudinum	Laguna Madre, Texas, USA	Floating fruit	1–10 days	N/A	<1–15	Kaldy and Dunton (1999)
Zostera marina	Chesapeake Bay, USA	Floating reproductive shoot	14 days	N/A	0.7–108.6	Harwell and Orth (2002a)
Zostera marina	Chesapeake Bay, USA	Seeds on sediment surface	N/A	5.96 ± 1.14	0.014	Orth et al. (1994)
Zostera marina	San Juan Island, Wasington, USA	Seeds on sediment surface	N/A	nd	Mean of 0.00127, max. distance <0.05	Ruckelshaus (1996)
Zostera marina	northern Wadden Sea, southwestern Baltic Sea	Floating reproductive shoot	nd	nd	33–54	Reusch (2002)
Posidonia coriacea	Perth, Western Australia	Seeds	N/A	17.1 ± 2.34	nd	Orth (1999)
Thalassia testudinum	Laguna Madre, Texas, USA	Floating seeds	<1–3 days	nd	0.06–3	Kaldy and Dunton (1999)
Zostera marina	New York, USA	Floating seed with air bubble	≥ 40 min	nd	0.001–>0.2	Churchill et al. (1985)
Enhalus acoroides	Bolinao reef system, Philippines	Floating seeds	14 h	10.0 ± 0.1	3.7	Lacap et al. (2002)
Thalassia hemprichii	Bolinao reef system, Philippines	Floating seeds	3.5 h	10.0 ± 0.2	18.2	Lacap et al. (2002)
Enhalus acoroides	Bolinao reef system, Philippines	Floating fruits	10.2 days	N/A	63.5 (estimated 400 km during typhoons)	Lacap et al. (2002)
Thalassia hemprichii	Bolinao reef system, Philippines	Floating fruits	7.2 days	N/A	73.5 (estimated 300 km during typhoons)	Lacap et al. (2002)
Enhalus acoroides	Bolinao reef system, Philippines	Seeds on sediment surface	N/A	10.0 ± 0.1	0.2	Lacap et al. (2002)
Thalassia hemprichii	Bolinao reef system, Philippines	Seeds on sediment surface	N/A	10.0 ± 0.2	<0.1	Lacap et al. (2002)

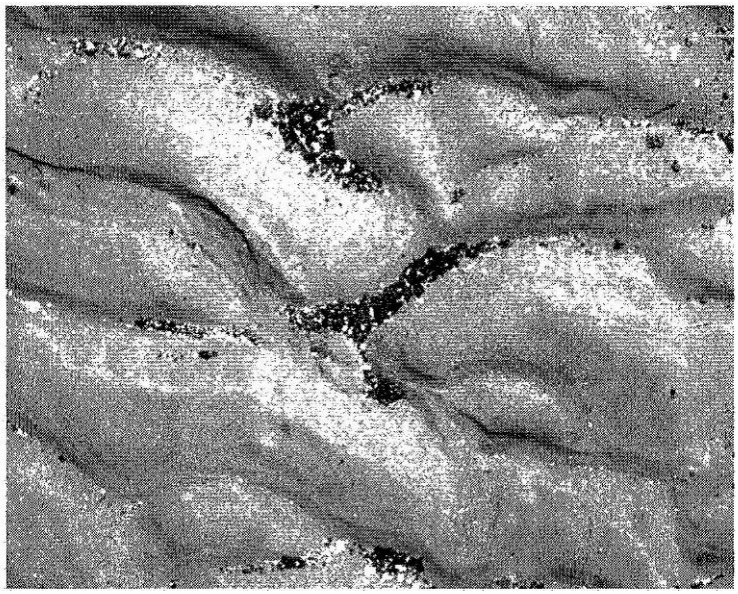

Fig. 4. Seeds of *Halodule uninervis* (black spheres) in troughs of small sand waves (scale c. 1:3). Seed densities can be as high as 114 seeds cm^{-2} in troughs but only 5 seeds cm^{-2} on hummocks (from Inglis, 2000b, reprinted with permission from Journal of Ecology).

movement (Figs. 4 and 5) (Orth et al., 1994; Luckenbach and Orth, 1999). However, seeds of some species may be moved along with bed load transport of sediments as observed with *H. uninervis* (Inglis, 2000b). Characteristics of seeds as they settle in the water column, especially seeds with varying sizes, shapes and biomass, as well as transport characteristics of seeds on the sediment surface at different flow velocities, will be important in dispersal distance estimates (Orth et al., 1994).

The movement of seeds from the parent plant has figured prominently in the recent debate about just how far a plant can disperse (Clark et al., 1998; Howe and Miriti, 2000). Dispersal distances of most terrestrial plant species are relatively small (10^1–10^2 m). However, these same species have been noted to migrate significantly faster (10^3 m or greater) than would be predicted by life history and seed dispersal characteristics alone, a phenomena first noted over 100 years ago related to the tree invasion and subsequent migration to the British Isles [i.e. Reid's Paradox of Rapid Plant Migration (Reid, 1899; Pitelka and the Plant Migration Workshop Group, 1997; Clark et al., 1998; Pakeman, 2001)].

In seagrasses, data on dispersal distances of seeds or fruiting structures, such as the detached reproductive shoots in *Zostera* or the buoyant fruits of *Enhalus*, *Posidonia* or *Thalassia*, are rare, but the emerging evidence suggests that these distances may be significantly greater than previously considered (Table 2) and may approach the dispersal distances of coconuts and mangroves, generally considered the best examples of long-distance dispersers. Surprisingly, observations made almost 100 years ago by Ostenfeld (1908) and Setchell (1929) suggested that long-distance dispersal could be attained by floating *Z. marina* reproductive shoots. Studies on the buoyancy potential (Table 1) of floating reproductive structures with viable seeds is a critical need in elucidating maximum dispersal distance that could be attained by various species of seagrasses. As with the terrestrial literature, interest in long-distance dispersal in now gaining attention with seagrasses (Inglis, 2000a; Harwell and Orth, 2002a).

Seeds of many terrestrial species have evolved adaptations to enhance dispersal (e.g. wings or pappi to enhance wind dispersed seeds and hooks or bristles to facilitate animal dispersed seed; Howe and Smallwood, 1982; van der Pijl, 1982). Studies on dispersal characteristics of seagrass seeds are rare but there are indications that several species may have evolved seed morphologies that allow the seed to be retained where it settles. *Posidonia* seeds are covered with a membranous coat, that in at least

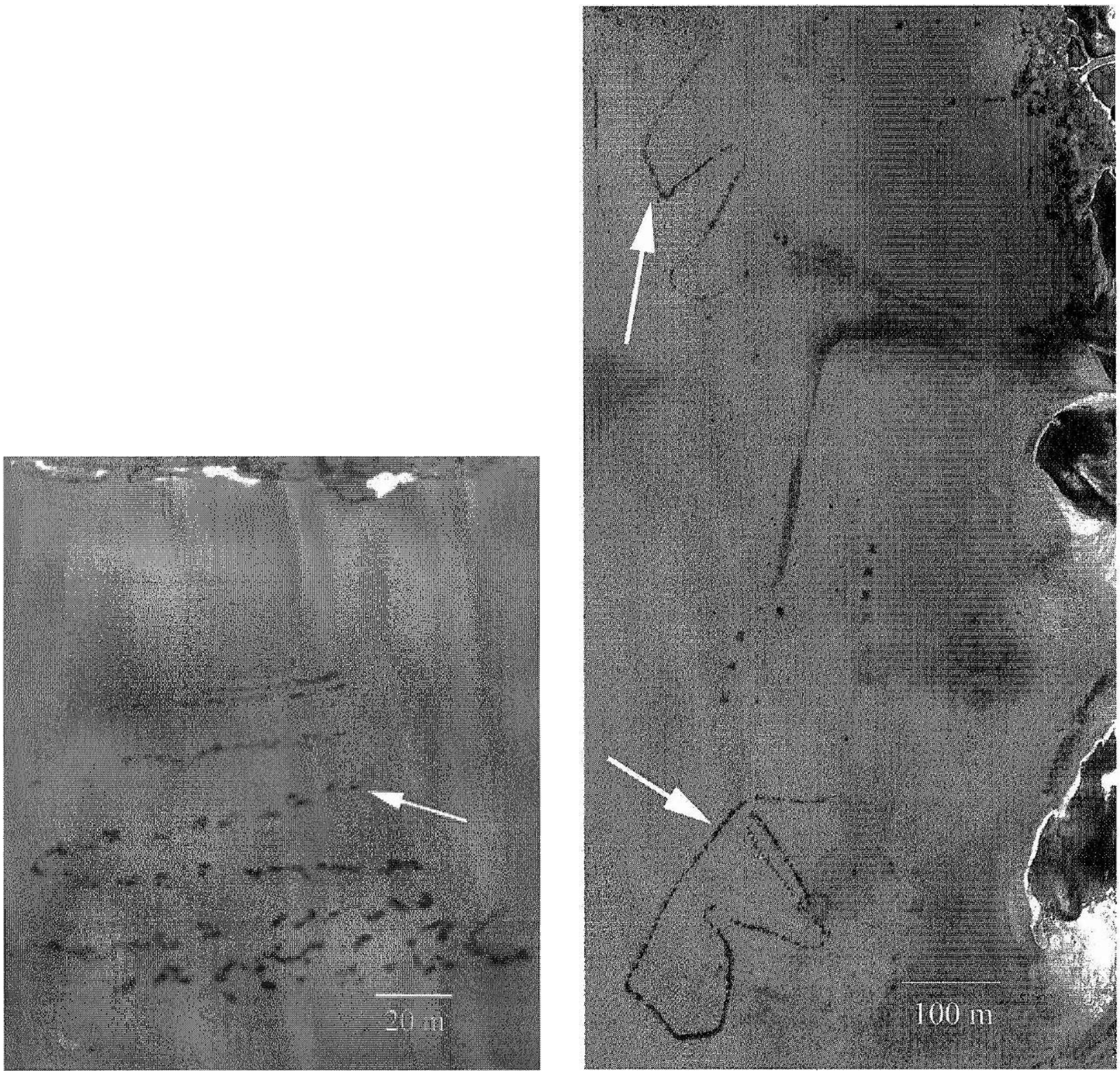

Fig. 5. Zostera marina seedling patterns (arrows pointing to dark bands) following seed broadcasting at two locations in Chesapeake Bay: Mumfort Island in the lower York River (A) and South Bay (B), a coastal lagoon in the Delmarva Peninsula. At Mumfort Island, approximately 250,000 seeds were broadcast in fall, 1988, in a 100 × 100 m plot from both the port and starboard stern of a boat as it made several paths across the plot (close inspection of each path reveals those seedlings arising from seeds broadcast from the port or starboard side of boat. The picture was taken in June, 1989, nine months after seeding. At South Bay, approximately 150,000 seeds were broadcast in fall, 1999, from a boat at two locations in a pattern that resulted in seedlings showing the design of a 'B' and 'W' in a picture taken in July, 2000, nine months after seeding. Seedling patterns result from seeds that settle rapidly and become rapidly incorporated into the sediment matrix.

one species, *Posidonia coriacea*, increases the fall velocity (Orth, 1999). Once settled onto the sediment surface the membrane may serve to retain the seed near where it settles by influencing hydrodynamics around the seed, minimizing disturbance by waves and currents, and facilitating burial. Seeds of *Phyllospadix* have two arms with stiff bristles that facilitate entanglement in a filamentous algae (Turner, 1983; Blanchette et al., 1999). Similarly, seedlings of *Amphibolis* have a barbed base that can catch onto algal filaments. While seeds of other species may appear at first to have no adaptations to either enhance or limit dispersal, we hypothesize that the distinct morphology of seeds influences dispersal distances. For example, the tests of *Halophila* seeds are highly sculptured with peg-like (*Halophila spinulosa*), or honeycombed projections (*Halophila ovalis*) that may aid seed dispersal (by trapping air bubbles), burial or shedding of the test during germination (Birch, 1981). During germination, a large mass of fine, long hairs develops on the seed surface of *H. spinulosa* that appear to anchor it in the sediment before the radicle emerges (this process also appears to occur with *Thalassia testudinum* seedlings). The actual functional purpose of seed coat ornamentation in *Halophila*, and that displayed on seed coats in other seagrass genera (e.g. *Zostera*), is still to be determined. *H. uninervis* produces smooth, hard, oval achenes that lack obvious sculpturing or projections on the pericarp. This morphology appears to be particularly amenable to tumbling dispersal in mobile sediments, where the seeds accumulate in large numbers within small pits and depressions (Fig. 4) (Inglis, 2000b). In terrestrial plants, accessibility to suitable germination sites has been shown to be dependent on seed morphology (smooth vs. rough surfaces and size; Harper, 1977), but no studies have been conducted to date with seagrasses to test similar hypotheses about the functional importance of seed morphology and size.

Seed dispersal in seagrasses can be influenced by the position of seed release from the parent plant. Within the seagrass genera, seeds can be released either from elevated inflorescences, or at or just below the surface of the sediment (Table 1). For those species that release seeds below the sediment surface (*Halophila*, *Cymodocea,* and *Halodule*) dispersal distances from the parent plant may be on the scale of centimeters. These genera also have highly persistent seed banks, so this strategy may have evolved to maximize seed dispersal in time, rather than space (Venable and Lawlor, 1980). In this case, appropriate microsites for germination and initial seedling establishment may become available when the parent plants are disturbed or where storms or intense biotic activity (rays or manatees) cause plants, sediments, and seeds to be transported to secondary sites.

Seagrass seed dispersal can be controlled by both abiotic and biotic elements (Fig. 2). Wind and currents are important in transporting floating reproductive fragments or fruits long distances. Most measurements of seagrass propagule dispersal are indirect, involving multiplying some metric of flotation potential to speed of water flow. Harwell and Orth (2002a) showed that currents alone could move a *Z. marina* reproductive fragment up to 23 km in a single 6 h tidal cycle and strong winds could significantly alter that distance. Small patches of *Z. marina* have been found at distances of up to 108 km from the nearest source of donor material and Harwell and Orth (2002a) hypothesized that these derived from seeds carried by floating reproductive fragments. Kaldy and Dunton (1999) calculated dispersal distances of up to 3 and 15 km for seeds and fruits, respectively, for *T. testudinum*, while Lacap et al. (2002) calculated dispersal distances up to 3.7 and 63.5 km for seeds and fruits, respectively, for *Enhalus acoroides*, and up to 73.5 km for fruit of *Thalassia hemprichii*. Lacap et al. (2002) also postulated that fruits of *Thalassia* and *Enhalus* could be transported 300–400 km, respectively, during typhoons. Kendall et al. (2004) suggest that hurricanes may be responsible for expansion of a *Syringudium filiforme* meadow in St. Croix, US Virgin Islands by enhancing seed and seagrass fragment dispersal.

Human activities can also influence long distance dispersal if reproductive fragments are moved in ballast water of ocean going vessels, incorporated as wet packing material for shipment of live specimens, or attached to boat trailers. For example, the Japanese eelgrass, *Zostera japonica*, is thought to have been introduced accidentally to the United States west coast in the early 1900s as seeds transported in live shipments of Japanese oysters (Harrison and Bigley, 1982). Lipkin (1975) suggested that ship transport was a source of *Halophila stipulacea* into the eastern Mediterranean after Isthmus of Suez was breached. Nienhuis (1983) suggested the rapid spread of *Z. marina* into Lake Grevelingen in the Netherlands was a result of the closure of the estuary, which may have allowed floating reproductive shoots to be retained within the closed estuary rather than being exported.

Biotic agents such as waterfowl, especially migrating waterfowl, manatees, dugongs, or fish also have the potential to move seeds relatively long distances if they are ingested (Baldwin and Lovvern, 1994; Figuerola and Green, 2002; Figuerola et al., 2002; 2003). Seagrass species with relatively hard seed coats (e.g. *Halodule*) may survive the passage through the guts of these species better than those with softer seed coats (e.g. *Zostera*). Figuerola et al. (2002) found that germination of *Ruppia maritima* seeds was enhanced by passage through the guts of ducks but was species specific and probably related to gut structure (i.e. type of gizzard). An important but overlooked aspect may be the timing of availability of viable seeds and the presence of migrating waterfowl. For example, in Chesapeake Bay, USA, *Z. marina* seeds are produced in May and June and germinate in late November before wintering waterfowl are present, making it unlikely they could disperse seeds (Orth and Moore, 1986; Moore et al., 1993). Knowledge of seed release and germination periods coupled to an understanding of the feeding strategies of waterfowl that inhabit an area, will be important in elucidating the role of waterfowl in seagrass seed dispersal. In more intensively grazed meadows, the feeding activities of these large herbivores may actually stimulate seed production and germination (Peterken and Conacher, 1997). The decline of many of these large herbivore species, because of over-harvesting or habitat destruction (Jackson et al., 2001), could have implications for the natural development of new seagrass beds distant from the original parent and, ultimately, for the gene flow and genetic diversity of the different populations.

Disturbance of a seagrass bed by biotic (e.g. turtles, manatees or fish) or abiotic (e.g. storms) can result in reproductive fragments being ripped and exported from the bed. Patterson et al. (2001) examined the biomechanical properties of how *Z. marina* reproductive shoots become fragmented. They suggested that the characteristics of how a reproductive shoots breaks potentially allows for dispersal of some reproductive fragments with viable seeds while allowing some seeds to be retained within the bed for self-maintenance.

Biotic agents can also limit primary dispersal of seagrass seeds. Reproductive shoots carrying viable *Z. marina* seeds have been found cemented into the tube cap of the common tube-building polychaete, *Diopatra cuprea* (Harwell and Orth, 2001). Drifting plant fragments appear to be entrained into the tube cap and subsequently incorporated into the construction of the tube. However, this retention may be important in establishment of beds distant from a source if *Diopatra* inhabiting suitable but unvegetated bottom captures fragments that have floated from afar. In northern Australia, seagrass seeds accumulate within trails excavated in the meadows by feeding dugongs (Inglis, 2000b).

V. Seed Recruitment and Seedling Establishment

While studies have shown seagrasses can produce large numbers of seeds, those few studies that have followed through have reported a very low rate of seedling establishment (Table 1). Rarity of seedlings at a site may be due to recruitment or seed limitation (the inability of propagules to reach a suitable site or too few propagules being produced) or microsite limitation (the absence of suitable 'safe' sites) (Harper, 1977; Eriksson, 1989; Eriksson and Ehrlen, 1992). Recruitment limitation can also arise if hydrodynamic conditions, such as currents or winds, are unable to deliver a propagule to a site, or if there is a distinct physical barrier to dispersal such as a land bridge. While Crawley (1990) argued that microsite limitation is predominant in plant populations, Eriksson and Ehrlen (1992) suggested that recruitment for clonal plants is the result of both microsite and seed availability.

The sediment surface may be viewed as a patchwork or 'lattice' of sites that may be considered safe and unsafe for germination (Harper, 1977) with seeds having to pass through a suite of environmental obstacles (an 'environmental sieve', Harper, 1977), from the time of release to the time of germination at a 'safe' site. Harper (1977) defined a 'safe' site as a zone where seeds find the required stimuli and resources to germinate and grow, and where mortality factors are absent. What constitutes a 'safe site' in seagrass systems may, in part, be related to the topographic complexity of the bottom created by biotic (pits and burrows of animals) or abiotic (sand ripples) factors and how rapidly a seed can be buried before it is eaten or washed out to an unsuitable site, leading to the patterns noted in Fig. 5.

Recruitment behavior of clonal plants has been classified as species that exhibit either repeated sexual recruitment (RSR) or those species whose seeds are only responsible for the initial establishment (initial seedling recruitment, ISR) of a population (Eriksson, 1989). Inglis (2000a) suggested that that seagrasses that produce large fleshy fruits (e.g. *Thalassia*, *Posidonia*) might be expected to exhibit an ISR strategy based on the evidence that seedling recruitment had been rarely recorded in these species. However, more recent evidence for *T. testudinum* in Florida, USA, (Whitfield et al., 2004), *T. hemprichii* and *Enhalus acoroides* in the Philippines (Olesen et al., 2004) and both *P. coriacea* and *Posidonia australis* in Australia (Kendrick et al., 1999, personal communication; Orth, personal observation) shows that seedling recruitment for these large species may occur more frequently than previously thought, suggesting that an RSR strategy may be more common in these seagrasses.

Pathogens, predation, inter- and intra-specific competition, nutrient limitation, movement to unsuitable germination sites, smothering by organic debris (e.g. macroalgae; Hauxwell et al., 2001; 2002; Cambridge et al., 2002) or simply failed germination can all account for seed losses (Harper et al., 1965; Chambers and MacMahon, 1994). Some of these factors may be density-dependent, although one study with *Z. marina* (Orth et al., 2003) did not show density dependence. One process in particular, seed predation, has been shown to be highly significant in terrestrial environments across broad latitudinal gradients and can account for complete loss of seed production in some systems (Janzen, 1971; Harper, 1977; Wenny, 2000). The few studies to date suggest that predation may be an important process governing the production, survival, and establishment of seagrass seeds, and can occur at both the pre-dispersal phase as well as the dispersal phase (Holbrook et al., 2000; Piazzi et al., 2000; Balestri and Cinelli, 2003) (Table 3).

Terrestrial studies have shown higher seed predation under or near the parent plant (Janzen, 1970; Connell, 1971; Harms et al., 2000) and while studies with animals have demonstrated higher predation rates with decreasing latitude, Moles and Westoby (2003) found no evidence of higher seed predation towards the tropics. In addition, while larger seed sizes might be expected to have higher predation rates, Moles et al. (2003) found either no or weak relationships between seed mass and post-dispersal survival rates. There have been no studies on latitudinal gradients in seed predation in seagrasses, nor predation studies on seeds of different sizes, but a recent study by Orth et al. (2002) found predation on *P. australis* seeds in seagrass beds in Western Australia higher in seagrass compared to adjacent bare sand (Fig. 6) suggesting similar advantages to being away from the parent as hypothesized for terrestrial species.

The presence of a seedling represents the end point of dispersal, and the processes that influence the establishment of a seedling from a seed are often diverse and complex (Wenny, 2000; Wang and Smith, 2002). Even when a seed escapes direct agents of mortality and can germinate in a suitable ‘safe site’, its success is not ensured. Duarte and Sand-Jensen (1990) found seedling appearance for *Cymodocea nodosa* in the Mediterranean far exceeded patch formation (470 seedlings ha^{-1} $year^{-1}$ vs. 45 patches ha^{-1} $year^{-1}$, respectively). Olesen and Sand-Jensen (1994) also found high rates of seed recruitment in *Z. marina* in Denmark (0.16–0.76 m^2) but significant mortality of small patches with less than 24% of the studied cohorts remaining as individual patches 1.5–2.5 years later. Olesen and Sand-Jensen (1994) suggested that improved anchoring, mutual physical protection and physiological integration among shoots were responsible for greater success of larger patches. Duarte and Sand-Jensen (1996) showed that nutrient deficiency may be a significant source of mortality in seedlings. Once its stored reserves are exhausted, a young seedling must be able to extract sufficient nutrients from the surrounding sediment for maintenance and growth. In many sites, the availability of nitrogen and phosphorus may be severely limited by high metabolism within well-oxygenated sediments or the presence of adult competitors as suggested by Olesen (1999) who found the majority of seedlings within an established *Z. marina* bed in Denmark were shaded out during summer.

Biotic agents can negatively influence seedling establishment. Dumbauld and Wyllie-Echeverria (2003) showed that the long-term survival of *Z. japonica* seedlings in Washington, USA, were influenced by the burrowing activities of thalassinid shrimps. Although several studies have documented bottlenecks in seedling survival (Inglis, 2000a; et al., 2003), the reasons behind these failures require greater examination.

VI. Seagrass Conservation and Restoration: Utility of Seeds

Increasing recognition of the numerous ecological services provided by seagrasses (Costanza et al.,

Table 3. Summary of seagrass fruit/seed predation studies.

Species	Location	Field or Laboratory	Predator	Results	Reference
Zostera marina	Chesapeake Bay, USA	Field	*Callinectes sapidus* (crab)	65% of seed losses in exclosure/inclosure caging experiments caused by predation	Fishman and Orth (1996)
Zostera marina	Long Island, NY, USA	Laboratory	Crustaceans, molluscs, and fish	crustaceans and 1 mollusc species consumed or damaged up to 93% of seeds, which declined when alternative food sources were available	Wigand and Churchill (1988)
Zostera marina and *Z. caulescens*	Otsuchi Bay, Japan	Field	*Zeuxo* sp. (tanaid crustacean)	14 and 27% of seeds in spathes in *Z. marina* and *Z. caulescens,* respectively, were bored by the tanaid	Nakaoka (2002)
Posidonia oceanica	Livorno, Italy	Field and Laboratory	*Sarpa salpa* (sparid fish)	More mature inflorescences found in caged (37.5%) vs. uncaged (10.1%). Fish grazed entire reproductive structures.	Piazzi et al. (2000)
Posidonia oceanica	Livorno, Italy	Field	Unknown	84% of developing inflorescences damaged by herbivores. Protected plots produced 37.5% more fruits.	Balestri and Cinelli (2003)
Enhalus acoroides	Bolinao reef system, Philippines	Field	Alpheid shrimp	seeds collected and brought into shrimp's burrow within minutes	Lacap et al. (2002)
Zostera capricorni	Moreton Bay, Queensland, Australia	Field	*Penaeus esculentus* (shrimp)	seeds made up to 13% of the ash-free dry weight of the prawns diet only in Nov. when seeds were available	Wassenberg (1990)
Posidonia australis	Western Australia	Field	Unknown	Higher daily proportional mortality of seeds tethered in seagrass (34–53%) compared to bare sand (3–20%) at 5 sites.	Orth et al. (2002)
Phyllospadix torreyi	Santa Barbara, CA, USA	Field and Laboratory	*Pugettia producta* (crab), *Pachygrapsus crassipes* (crab), *Idotea resecata* (isopod)	Predation on seeds prior to release fom the spadix was low (7–24%). 10–50% of dispersed seeds caught in traps were damaged by predators.	Holbrook et al. (2000)
Phyllospadix torreyi	Santa Catalina Island, CA, USA	Field	*Girella nigricans* (opaleye fish)	13–22% of male spadices were bitten while female spadices showed no damage.	Williams (1995)

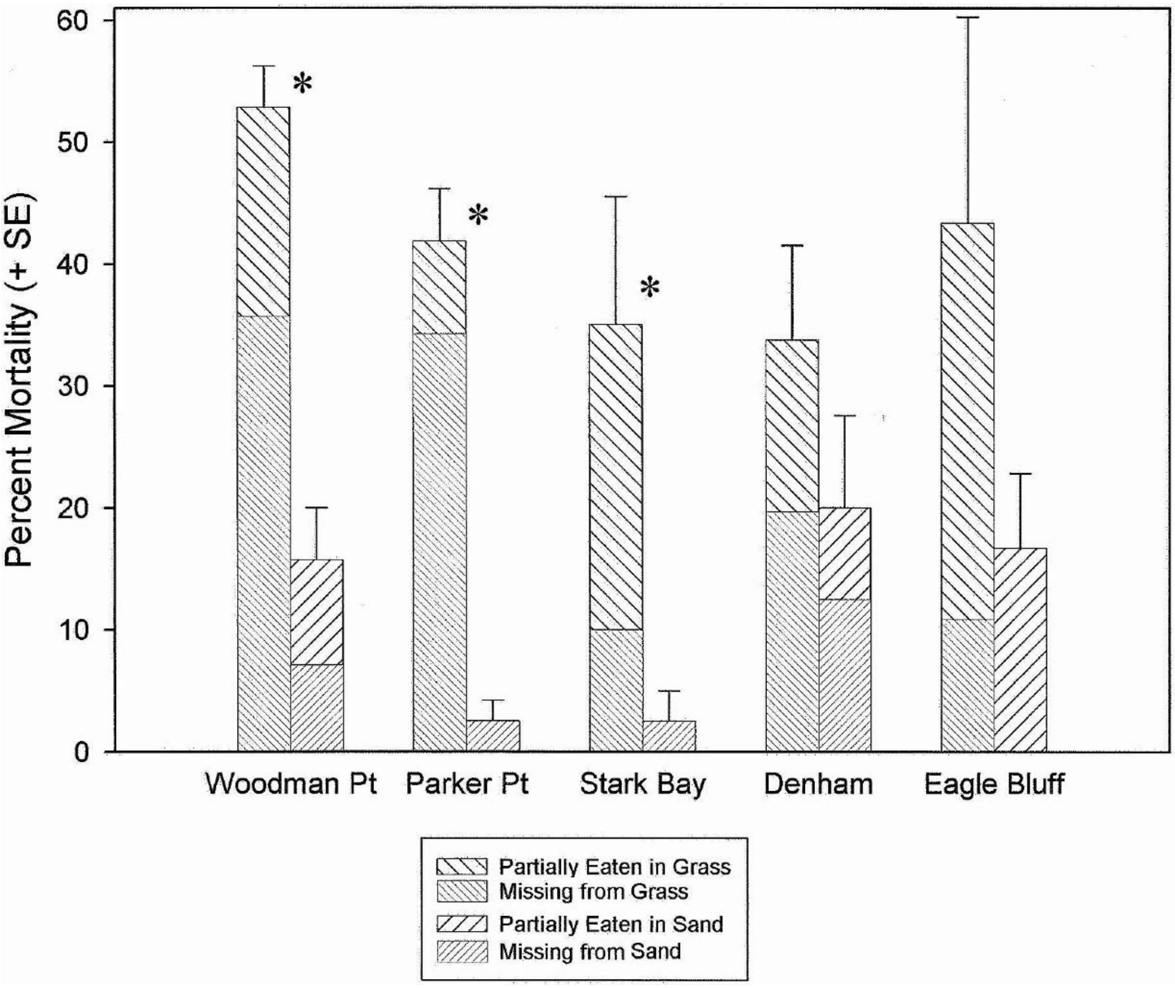

Fig. 6. Proportional mortality of *Posidonia australis* seeds in seagrass beds vs. bare sand at the five sites (Mean + SE) in Western Australia. Average mortality is divided into two components representing the overall proportion of partially eaten seeds and completely removed seeds for each site and each substrate. Asterisks indicate significant differences between the two habitat types (from Orth et al. 2002).

1997; Beck et al., 2001; Heck et al. 2003; Kenworthy et al., Chapter 25) and their concurrent decline due to anthropogenic inputs of sediments and nutrients (Short and Wyllie-Echeverria, 1996) has prompted scientists and resource mangers to explore ways to protect existing beds and restore disturbed communities. Because seeds are more likely important in establishing new patches of seagrasses (Olesen and Sand-Jensen, 1994; Plus et al., 2003; Olesen et al., 2004) than drifting adult plants (Duarte and Sand-Jensen, 1990; Ewanchuk and Williams, 1996), protection of existing beds, particularly those that are the source of large numbers of seeds, should be a priority for resource managers. Also, if there is no density dependence in seed survival and initial seedling establishment (Orth et al., 2003) and propagules of most species can disperse large distances, all beds, regardless of their size and density, should be protected. Alternatively, if studies show that, for some species, some meadows are significant sources of sexual propagules while others are significant sinks (e.g. upcurrent vs. downcurrent, intertidal vs. subtidal populations), it may be possible to identify areas that should receive greater priority for conservation than others (see Kenworthy et al., Chapter 25).

Seagrass restoration projects have been attempted over the last two decades with a variety of techniques and variable success (Fonseca et al., 1998).

Most programs have involved the transplantation of adult ramets; use of seeds has been rare (Fonseca et al., 1998). We believe that seeds should be incorporated into future restoration programs for a number of reasons. Many species produce regular crops of large numbers of seeds that can be easily harvested and stored. However, there is great variation among species and meadows in the regularity with which seeds are produced. Some of the larger tropical seagrasses appear to produce seeds infrequently (see Duarte et al., 1997). Flowering in *Posidonia oceanica*, the dominant seagrass species in the Mediterranean, is apparently very rare in most locations (Balestri and Cinelli, 2003). Because of this variation, identification of suitable source populations and their reproductive phenology is a necessary first step. Harvesting seeds has less impact on a donor bed than harvesting adult plants and may have no significant impact on long-term survival of the donor bed. However, studies on the impacts of long-term removal of seeds from an area are non-existant and if restoration programs begin to target areas for seed removal, it will be important to monitor not only the donor beds but adjacent areas that may be recipient sites for seeds that were exported from surrounding areas. Meadows created from transplanted ramets tend to be genetically more homogenous, grow slower, produce fewer seeds and have poorer rates of germination than more genetically diverse stands (Williams, 2001). Although natural seed mortality is generally high (Harrison, 1993; Orth et al., 2003), the potential exists for increasing survivorship with innovative techniques (e.g. Harwell and Orth, 1999). Seeds have the potential for accelerating or enhancing restoration by establishing new patches, adding to slowly recovering areas, or increasing species and genetic diversity of meadows. Using seeds, possibly in conjunction with adult plants, may prove to be more cost and labor effective than using adult plants in some seagrass species.

VII. Conclusions and Emerging Paradigms

Seed ecology represents an exciting opportunity for seagrass research. Many of the intriguing issues discussed in terrestrial environments are likely to be applicable for seagrass species. Seeds are likely to be significantly more important in the dynamics of bed development than previously believed. However, generalizations may fail in extreme ranges of populations where flowering may be limited and asexual propagation considered more important in meadow maintenance and spread (Billingham et al., 2003). New paradigms will emerge as the field evolves and as questions are answered about the role seeds play for different species in determining dispersal, genetic diversity and evolution (Reusch, 2002).

A. Dispersal

Dispersal, in particular, has been the subject of a number of recent in-depth review articles in the terrestrial literature, pointing to challenging areas of research such as managing pristine, degraded or restored areas as sources of diaspores, recognition of sites as sources or sinks of propagules, etc. (Clark et al., 1998; Howe and Miriti, 2000; Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Higgins et al., 2003; Levin et al., 2003). Emerging technologies are allowing us to address previously intractable questions about dispersal and connectivity within populations (e.g. molecular genetic techniques, stable isotopes, radioactive labeling, fluorescent microspheres) (Wang and Smith, 2002). The use of ecological simulation models to examine seagrass reproduction (Bearlin et al., 1999; Harwell, 2000) and geographic information systems (GIS) to examine patch dynamics (e.g. Wilcox et al., 2000; Duarte et al., Chapter 11) can be valuable tools for bridging the gap between theoretical and actual population and metapopulation dynamics. Long-distance dispersal has now been demonstrated in at least four species, and it is possible that this phenomenon will be found in most, if not all, seagrass genera although the mechanisms may be dramatically different. We predict that future studies will demonstrate that seeds on the sediment surface do not move far from where they settle except as a result of extreme catastrophic events.

B. Dispersal Processes

Understanding the different aspects of dispersal (Phase I and II, Chambers and MacMahon (1994) will be very important in understanding actual dispersal distances and the speciation of seagrasses as populations which may not be as isolated in geologic history as once thought. Research should focus on the relative proportion of seeds that are both retained within a bed as well as exported, and the fate of each component. Mechanisms of dispersal need to be considered now that it appears seagrasses are capable of long-distance dispersal, especially 'nonstandard' mechanisms (Higgins et al., 2003). This would be especially true from an historical perspective if some processes have been lost or minimized, e.g. potential loss from large reductions of turtles and sirenians due to overfishing that could have eaten seeds and excreted them long distances from feeding sites (Jackson et al., 2001). Waterfowl may be an underestimated mechanism that could influence local, as well as regional, population dynamics (Figuerola and Green, 2002; Figuerola et al., 2002).

Terrestrial seeds have developed various structures to enhance dispersal, e.g. wings, barbs, pappi. While some species have developed structures to facilitate entrainment (e.g. barbs of *Phyllospadix* seeds, or the hooked bases of *Amphibolis*), seagrass seeds appear to be remarkably simple in ornamentation suggesting seeds have not evolved mechanisms for dispersal. It is entirely possible that the ornamentation seeds do have functions more to retain seeds where they settle, e.g. the 'membrane' surrounding *Posidonia* seeds.

Many dispersal studies have emphasized how far a seed can travel (the tail of the dispersal curve). However, understanding the shape of the dispersal curve has important consequences for not only the rate of spread of a species, but also metapopulation dynamics (Clark et al., 1998; Williamson, 2002). Future studies with seagrass dispersal, both empirical and modeling, need to consider both aspects. As Williamson (2002) concluded "it's the tail that wags the dog."

C. Mating Systems

Greater study of seagrass seeds should also offer some useful insights into the evolution of angiosperm mating systems. Of particular importance are recent theoretical treatments of the seed-shadow handicap in dioecious species (Heilbuth et al., 2001). Because only female plants produce seeds in dioecious populations, the total number of seed bearers is at least half that of an equivalent sized population of co-sexual species. Maintenance of dioecious species in the presence of hermaphroditic competitors, therefore, requires that this disadvantage is overcome by: (1) greater fecundity per plant, (2) increased division of labor between the sexes, (3) greater offspring vigor (as a result of reduced inbreeding depression), and/or (4) more broadly dispersed seeds to escape the densely populated seed shadows around maternal dioecious plants (Heilbuth et al., 2001). The predominance of dioecy in modern seagrasses points to some unique evolutionary pressures that have favored the retention of separate sexes (Waycott et al., Chapter 2). Further comparison of dioecious and co-sexual species may provide clues as to whether a seed-shadow handicap exists in these clonal species and, if it does, what traits offset the disadvantages associated with dioecy.

D. Adult–Seedling Interactions

The importance of adult–seedling interactions in terrestrial plant assemblages argues for greater attention to these issues in seagrass populations (Olesen, 1999; Duarte et al., Chapter 11). Although long-distance dispersal has been demonstrated for seagrass seeds, it is likely that some proportion of seeds do not travel outside the stands that produce them. The longevity of some seagrass clones (Reusch et al., 1999) may mean that seed production and suitable microsites for recruitment occur infrequently in space and time if clones are sufficiently dense and continuous to compromise seedling survival. At this stage, it is unclear if seedling germination, survival and growth is inhibited by the presence of existing adults (through more efficient utilization of light and nutrients by adults) or facilitated by them (through the provision of shelter, anchorage and the greater organic content in the sediments of existing stands). Given the variety in dispersal strategies and adult size and longevity, we predict that the answers to these questions will also vary significantly among species.

E. Recruitment

Understanding the roles of recruitment limitation vs. microsite limitation in seagrass species is also important for planning appropriate conservation strategies. These questions can only be addressed through seed sowing experiments, either through seed augmentation where sown species are residents of the target community, or seed introduction, where sown species are not part of the community (Turnbull et al., 2000; Orth et al., 2003). Predation and genetic stock may be important aspects governing seed distribution and viability in some species. Studies are needed to determine if seagrass dispersal strategies, like those of terrestrial angiosperms, have evolved to cope with higher rates of predation and disturbance within existing beds (Harms et al., 2000; Howe and Miriti, 2000).

F. Seed Stocks

We are only beginning to gain insight into the importance of genetic variation to the long-term success of clonal populations. In some species of seagrass (*Z. marina*), there appears to be a strong relationship between genetic diversity and plant vigor (Williams, 2001), while others maintain vast sexual populations that have almost no detectable genetic variation (*Amphibolis antarctica*; Waycott et al., 1996; Waycott et al., Chapter 2). Understanding the role of seeds in the long-term dynamics of seagrass populations has taken on an extra sense of urgency with predictions of present and future global change (Short and Neckles, 1999; Ferriere et al., 2000; Twilley et al., 2001; Scavia et al., 2002; Johnson et al., 2003; Kenworthy et al., Chapter 25) and with the fragmentation of habitats into isolated patches that theoretically could result in lower overall seed sets (Reusch, 2003). The emerging importance of seeds to the long-term dynamics of seagrass populations, and perhaps even more importantly in creating new patches distant from parent stock or in the recolonization of disturbed areas rather than maintaining existing, well-established beds (Olesen, 1999; Olesen et al., 2004), means that scientists and managers must place greater emphasis on conserving existing beds to provide a seed bank, and possibly in exploring ways to use seeds to restore areas that may have lost seagrass and are far away from potential seed sources.

Acknowledgments

We appreciate constructive comments provided by S. Marion, J. Vermaat, and J. Ackerman and several anonymous reviewers. Contribution number 2654 from the Virginia Institute of Marine Science. Fig. 3e reprinted from *Aquatic Botany*, vol. 10, de Cock, A. W. A. M., Development of the flowering shoot of *Zostera marina* l. under controlled conditions in comparison to the development in two different natural habitats in The Netherlands. 99–113 (1981) with permission from Elsevier.

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Chapter 6

Seagrass Beds and Coastal Biogeochemistry

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I. Introduction

Seagrasses develop extensive beds at the interface between the water column and sediment in tidal or subtidal environments. The height of seagrass canopy ranges from a few centimetres to more than a meter (Koch et al., Chapter 8), and seagrass rhizospheres may penetrate from centimetres (e.g. *Halophila sp*; Duarte et al., 1998) to a few meters (e.g. *Posidonia oceanica;* Mateo et al., 1997) into the sediment, depending on the species. Seagrass beds may support large above- and below-ground biomasses (Fig. 1), and they rank amongst the most productive marine primary producers (Duarte and Chiscano, 1999; Mateo et al., Chapter 7). The metabolic activities and the structure of seagrass beds modify the physical and chemical conditions of the water column and sediments of the areas colonized. For instance, seagrass metabolism affects carbon and nutrient dynamics in coastal areas (Mateo et al., Chapter 7; Romero et al., Chapter 9), as well as oxygen concentration in the water column (Larkum et al., Chapter 14) and sediments (Borum et al., Chapter 10). The structure of seagrass canopy, for instance, modifies water current velocity and waves, enhancing sedimentation of suspended particles (Koch et al., Chapter 8), and preventing sediment resuspension (Gacia and Duarte, 2001). Similarly, the dense network of rhizomes and roots effectively retains the sediments produced by, and deposited in, seagrass rhizospheres.

The effects of seagrass beds on the physical and chemical conditions of the areas colonized constrain benthic microbial communities, and, thus, the processes involved in the mineralization of organic matter and regeneration of nutrients in coastal areas. Seagrass beds, therefore, play an important engineering role (*sensu* Jones et al., 1997) in controlling coastal biogeochemistry. The input of organic matter and the accumulation of seagrass detritus in the sediments increase the amount of microbial substrates in the sediments (Gacia and Duarte, 2001), and, due to the relative refractory composition of seagrass detritus as a result of the high

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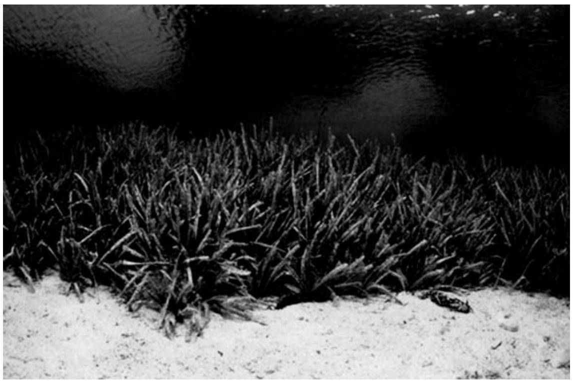

Fig. 1. View of a *Posidonia oceanica* meadow at 4 m depth in Cabrera (Balearic Islands, Spain) at the transition with the unvegetated sea-floor. (Photograph by E. Ballesteros).

content of structural compounds (e.g. lignin) in seagrass leaves, roots, and rhizomes (Vichkovitten and Holmer, 2004), the decomposition of seagrass detritus may only take place when nitrogen and phosphorus is supplied from other sources to the microbial community (Pedersen et al., 1999; Mateo et al., Chapter 7). There is thus an important competition between bacteria and seagrasses for nutrients, which may have large implications on the flux of nutrients across the sediment–water interface and this may affect seasonal patterns of nutrient availability in the water column. Due to the enhanced microbial activity in seagrass sediments, oxygen as an electron acceptor may be rapidly exhausted and anaerobic processes may take over the mineralization of organic matter (Holmer and Nielsen, 1997). As the availability of sulfate is high in the marine environment, sulfate reduction, and thus sulfide production, is often the most important anaerobic process in the sediments (Canfield et al., 1993). High sulfide production may affect growth and thus performance of seagrass meadows due to anoxia and sulfide toxicity (Borum et al., Chapter 10).

In this chapter, we review the role of seagrass beds on coastal biogeochemistry, (1) by examining their effect on particulate and dissolved materials (i.e. organic matter, dissolved inorganic carbon, carbonates, and gases) in the water column and sediments of coastal areas, and (2) by examining the processes involved in mineralization of organic matter and nutrient cycling in sediments colonized by seagrasses. The effect of seagrass beds on ambient nutrient pools is reviewed in detail in Romero et al., Chapter 9.

II. Role of Particulates and Dissolved Material

A. Effects of Seagrasses on Suspended Particle Load

Seagrass beds trap particles suspended in the water column via direct and indirect mechanisms. Leaf canopy indirectly enhances deposition of suspended particles by its interaction with water flow (see Koch et al., Chapter 8), which favours sedimentation rate (Gacia et al., 1999) and decreases resuspension of deposited particles on seagrass sediments (Gacia and Duarte, 2001). Yet, seagrass communities directly trap particles suspended in the water column. Two processes are responsible for direct particle trapping within seagrass beds: active filtering of the particulate material by the suspended feeders associated with the plant community (i.e. macro suspension feeders or epibionts associated with the seagrass leaves) and passive adherence of the suspended material onto seagrass surfaces (mainly leaves).

Abundance and biomass of macro suspension feeders (ascidians, sponges, and bivalves) tend to be higher in vegetated areas when compared to bare sand. This is due to a combination of factors, including enhanced rates of recruitment within plant canopies (Duggins et al., 1990; Boström and Bonsdorff, 2000), shelter from predators (Peterson and Heck, 2001), and higher abundance of food availability (Peterson et al., 1984). The abundance of epifaunal suspension feeders (hydroids, bryozoans, barnacles, amphipods, spirorbids, and protozoa) is also higher in seagrass beds than in bare areas, since seagrass canopy increases the available surface for colonization. Suspension-feeder communities have been shown to control phytoplankton populations in shallow-semi-enclosed environments (Buss and Jakson, 1981; Alpine and Cloern, 1992). Thus, active trapping of particulate organic matter (POM) from the water column by suspension feeders is expected to be higher in seagrass vegetated areas than over bare sediments.

There is very little quantitative information for direct particle trapping within seagrass canopies.

Abbreviations: %OC – percent particulate organic carbon in sediments; C/N – carbon/nitrogen; DIC – dissolved inorganic carbon; DO – dissolved oxygen; DOC – dissolved organic carbon; DOM – dissolved organic matter; DW – dry weight; PLFA's – phospholipid fatty acids; POM – particulate organic matter; SRR – Sulfate reduction rate

Studies in Western Australia (Lemmens et al., 1996) show that meadows of *Posidonia australis* were able to remove particles from the water column at much faster rates (approximately once a day) than unvegetated sand bottoms, where densities of macro suspension feeders and epibionts were found to be significantly lower. These removal rates of suspended particles were higher in *P. australis* and *Anphibolis antarctica* meadows than those of *Heterozostera tasmanica*. Species-specific differences in particle trapping rates may be due to differences in (a) canopy surface, which limits the area of substrate for epibiont colonization, and (b) leaf life-span, which sets the time window for epibiont colonization and, thus, constrains maximum epibiont biomass development (Cebrián et al., 1994). In addition, local environmental conditions may also restrict the development of filter feeding assemblages. In meadows of *P. australis* mentioned above, the epibionts were the dominant filtering community comprising 76% of the filtering activity of the system (Lemmens et al., 1996).

Direct particle trapping (including both passive and active mechanisms) has been reported for a seagrass mixed meadow in the Philippines (Agawin and Duarte, 2002). *In situ* incubations of seagrass and bare sediment areas with labelled phytoplankton and labelled inert particles demonstrated that water column clearance rate was four times faster within seagrass canopies than in bare sediments at 1.5 m depth. The authors estimated approximately 5% of the filtering capacity was due to the activity of protozoan epibionts (ciliates and amoeba-like organisms), whereas the largest fraction of particles was trapped by passive particle adherence on leaf surfaces.

Direct passive particle trapping has been estimated in seagrass meadows from South East Asia by quantifying the inorganic particles adhered to seagrass leaf surfaces across a wide range of sediment deposition rates (Gacia et al., 2003). These data did not quantify the particulate organic fraction of the passive trapping mechanisms but it provided rates of non-carbonate mineral clearance from the water column ranging from 0.1 to 0.6 g DW m^{-2} d^{-1} across meadows. These rates, however, represented only a minor fraction ($<1\%$) of the total non-carbonated inorganic material suspended in the water column, since the studied sites supported high siltation rates (Gacia et al., 2003). The clearance capacity of seagrass meadows by passive particle trapping depends on, for instance, seagrass productivity, local hydrodynamic conditions, and biomass and composition of the epibiont community, which is expected to enhance passive particle trapping by increasing the excretion of exopolymeric substances.

The above-mentioned mechanisms of particle trapping increases the particulate organic matter pool in seagrass sediments, since the structure of the seagrass leaf canopy and rhizosphere prevent resuspension and erosion of the material deposited on sediments interface.

B. Particulate Organic Matter in Seagrass Sediments

The positive effects of seagrass beds on particle deposition, together with the retention of most particulate organic matter produced by the bed itself (see Mateo et al., Chapter 7), enrich seagrass sediments with particulate organic matter (POM) compared to unvegetated areas. The percentage of POM in seagrass sediments often accounts for approx. 4% of sediment DW (e.g. Morse et al., 1985; Boschker et al., 2000; Hemminga and Duarte, 2000; Enríquez et al., 2001). However, the content of POM in seagrass sediments, in general, is lower than the organic content of coastal sediments colonized by other communities (e.g. mangroves and coral reefs; Kamp-Nielsen et al., 2002; Kennedy et al., 2004).

The sources of POM in seagrass sediments are seston, macroalgae, epibionts, and seagrass detritus. The relative importance of one or another source depends on different processes including meadow production, export, and decomposition rates (see Chapter 7 for extensive explanations), eutrophication, coastal erosion, and overall water flow in the area. Studies of the contributions of different sources of organic matter in seagrass sediments indicate that a significant fraction of the organic matter is refractory (i.e. 56–84% in a *P. oceanica* meadow; Danovaro, 1996), while only a minor proportion (18%) is recovered in the biopolymeric fraction (lipids, carbohydrates, and proteins). Danovaro (1996) traced the origin of the labile fraction of particulate organic matter and found that 25% of this fraction derived from benthic microphytoplankton. Other studies, however, revealed the importance of seston as organic matter source in seagrass sediments. Gacia et al. (2002) estimated that 43% of the organic carbon in the sediment of a 15 m depth *P. oceanica* meadow derived from the seagrass and epibionts, while the remaining fraction was provided by seston. Similar percentages

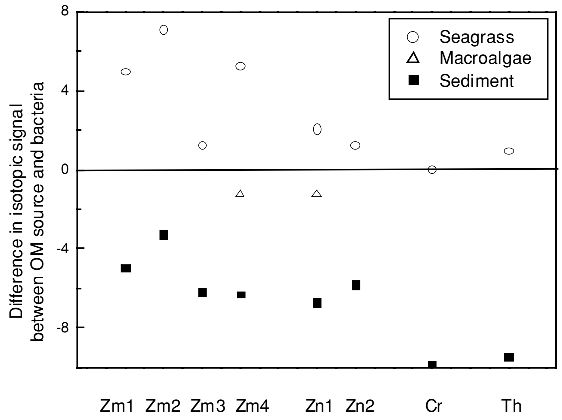

Fig. 2. Results of field studies of carbon sources used by bacteria in different seagrass beds. Stable carbon isotope ratios (δ^{13}C) of phospholipids fatty acids of sedimentary bacteria were compared with δ^{13}C ratios of the potential carbon sources found at the locations (seagrass, benthic macroalgae or sediment organic matter). Shown are the differences in the stable carbon isotope ratio between sediment bacteria and the potential carbon sources. Four studies of *Zostera marina* (Zm1-4), two studies of *Zostera noltii* (Zn1-2) and one study of *Cymodocea rotundata* (Cr) and *Thalassia hemprichii* (Th) are given. Carbon ratios of benthic microalgae were also analyzed at all sites, and were found to be important at the *Zostera* sites, but not for *C. rotundata* and *T. hemprichii*. Data are compiled from Boschker et al. (2000) and Holmer et al. (2001).

of seagrass material in sediment carbon pool (up to 30%) were observed in sediments colonized by *Thalassia hemprichii* in Kenya (Hemminga et al., 1994). Thus, seagrass material represents an important fraction of the organic matter accumulated in vegetated sediments. Seagrass-derived carbon, however, is not always the most important component in seagrass POM sediment pool, since seagrass meadows represent an important sink of organic matter from nearby ecosystems (Gacia et al., 2002; Kennedy et al., 2004).

The POM in seagrass beds enhances sediment microbial activity when compared with that in bare sediments (Danovaro and Fabiano, 1995; Danovaro, 1996; Donnelly and Herbert, 1999; Nielsen et al., 2001). Analysis of the isotopic composition of bacteria-specific lipids (phospholipid fatty acids, PLFA's) has shown that the microbial utilization of seagrass organic matter is important in oligotrophic sediments (Jones et al., 2003; Holmer et al., 2004), such as in *Cymodocea rotundata* and *Thalassia hemprichii* meadows in low-nutrient tropical sediments (Fig. 2). The isotopic carbon fractionation in the bacteria specific PLFA's extracted from the rhizosphere sediment in the two seagrass meadows were similar to the isotopic carbon fractionation of both seagrasses suggesting that seagrass detritus was an important organic carbon source for the bacteria (Holmer et al., 2001). There was no correlation between the benthic microalgae or other primary producers present in the seagrass meadows and the bacterial isotopic signal, suggesting that these carbon sources were not utilized to a large degree by bacteria. On the other hand, under more eutrophic conditions, seagrass detritus does not appear to be the most important bacterial carbon source. Under these conditions benthic microalgae, macroalgae, and phytoplanktonic detritus appear to be preferentially utilized by the bacteria probably due to their increased abundance under eutrophic conditions and higher lability compared to seagrass detritus (Fig. 2; Boschker et al., 2000; Holmer et al., 2004).

A fraction of seagrass detritus, mainly leaves with epiphytes, can be found accumulating in either depressions of the seafloor, near seagrass meadows, or on marine sediments further away, such as beaches, and small harbors (Hemminga et al., 1991; Romero et al., 1992; Fabiano et al., 1995; Hemminga and Duarte, 2000). Seagrass detritus has also been found in the sediments of emergent dunes in Mauritania (Hemminga and Nieuwenhuize, 1990) and Western Australia (Kirkman and Kendrick, 1997), and in the sediments of adjacent ecosystems, such as mangrove forests (Hemminga et al., 1994). Hence, seagrass beds provide POM to adjacent coastal areas, which is expected to influence biogeochemical processes and the structure of systems in the vicinity (see Bell et al., Chapter 26).

The effect of seagrass beds on POM sediment enrichment, however, changes during meadow development. Because production of seagrass detritus and seston deposition rate increase during seagrass colonization (Cebrián et al., 2000; Barrón et al., 2004), and the slow mineralization (Mateo et al., Chapter 7) of the seagrass detritus retained in seagrass sediments, seagrass sediments become POM enriched during the life-span of the meadow (Pedersen et al., 1997). For instance, total POM accumulated in the sediments colonized by *C. nodosa* at Alfacs Bay (E Spain) increased to 96.9 ± 37.9 g m^{-2} year^{-1} (Pedersen et al., 1997) during meadow development. Similarly, it has been demonstrated that export of seagrass detritus to adjacent coastal systems also increases as meadows develop (Cebrián et al., 2000). Detrital *C. nodosa* leaf export in established meadows was three-fold higher than that in young meadows (Cebrián et al., 2000). The role of seagrass beds as a sink, or a source of organic matter to adjacent sediments, therefore, varies during the colonization process.

C. Dissolved Organic Matter and Seagrass Beds

Seagrass beds release dissolved organic matter (DOM) by different mechanisms such as leaching (Mateo et al., Chapter 7; Romero et al., Chapter 9) and decomposition (Mateo et al., Chapter 7) of its own material, and active excretion of DOM by leaves and roots to the water column and to the sediment pore water (Benner et al., 1986; Findlay et al., 1986). To simplify, and because most of the studies on DOM release provide information only on the carbon fraction, we essentially focus on dissolved organic carbon (DOC) when referring to the soluble fraction of the organic matter associated with seagrasses.

The amount of DOC released by seagrasses has been measured in laboratory incubations for a number of species. Brylinsky (1977) reported that less than 5% of the inorganic carbon fixed by macrophytes is released as DOC. *Halodule wrightii* excretes less than 2% of the ^{14}C fixed to the water column (Wetzel and Penhale, 1979; Moriarty et al., 1986). However, the carbon released by the seagrass ecosystems can derive from the seagrass itself, from the epiphytes attached to the plant, and from the sediment. Penhale and Smith (1977) found that *Zostera marina* shoots with epiphytes released only 0.9% of the total carbon fixed as DOC, whereas DOC release by clean eelgrass shoots represented 1.5% of the total carbon.

In addition, part of the carbon fixed by seagrass leaves is translocated to below-ground organs and a fraction of it is released as DOC to the sediments. Blaabjerg et al. (1998) estimated that 2–4% of the total amount of carbon fixed by *Z. marina* was released as DOC into the rhizosphere. In *H. wrightii*, DOC release into the sediment accounted for 11% of the total ^{14}C fixed by the plant when plants were illuminated (Moriarty et al., 1986). These estimates, however, were obtained using ^{14}C technique which can underestimate the amount of DOC released by the seagrass ecosystems, as it only reflects the release of carbon recently incorporated by the plant without taking into account the release of DOC from carbon already stored in the plant.

Recently, net DOC production by seagrass ecosystems has been estimated *in situ* (e.g. Velimirov, 1986; Buzzelli et al., 1999; Ziegler and Benner, 1999a). Ziegler and Benner (1999a) reported that the net DOC release to the water column represented 10% of the net primary production in a *T. testudinum*-dominated community using *in situ* benthic chambers: in the light, this community released from 8 to 23 mmol C m^{-2} d^{-1} to the water column, while net DOC flux in bare sediment ranged from −26 to 10 mmol C m^{-2} d^{-1}. Net DOC release decreased during darkness in seagrass and bare sediments (Ziegler and Benner, 1999a). Similarly, Velimirov (1986) reported a higher DOC concentration within the *P. oceanica* meadow than above bare sediments, suggesting that most DOC in the water column may be produced by the seagrass community. Indeed, *P. oceanica* communities maintained a net release of DOC during a 1.5 year study, while the adjacent sediment oscillated between a sink or source of DOC depending on the time of the year (Barrón et al., unpublished data).

The magnitude and quality of the DOM released by seagrass communities varies seasonally. A *T. testudinum*-dominated community released DOC to the water column during the whole year, reaching a maximum in summer (Ziegler and Benner, 1999a). Similar seasonality in the amount of DOC released has been observed in *P. oceanica* beds (Barrón et al., submitted). The C/N ratio of DOM released by *T. testudinum*-dominated communities also exhibits seasonal changes. DOM fluxes were nitrogen depleted during early summer, when seagrass productivity was high, and nitrogen enriched during the late summer (Ziegler and Benner, 1999b). The seasonality in DOM nutrient quality may reflect seasonal changes among the processes (i.e. exudation vs. leaching) involved in DOM release to the water column (Ziegler and Benner, 1999b). Exudation most likely represents the dominant process for DOC release during periods of primary production, whereas leaching provides most of the DOC released to the water column during late summer, when net primary production is relatively low and seagrasses begin to senesce (Ziegler and Benner, 1999b).

The release of DOC from seagrass beds enhances bacterial activity both in the water column and the sediments. In oligotrophic systems (e.g. a subtropical seagrass bed), an increase of bacterial activity coupled to DOC production may out-compete phytoplankton and macrophytes for nutrients, hence shifting seagrass bed metabolism from autotrophic to heterotrophic (Ziegler and Benner, 1999a). In sediments, DOC is also rapidly accessible to bacteria and becomes available to higher consumers (Robertson et al., 1982). An experiment with *T. hemprichii* and *C. rotundata* showed that both seagrass species excreted DOC by below-ground tissues more than sufficient to fuel the anaerobic microbial activity (Holmer et al., 2001). Also, the activity of sulfate-reducing bacteria is coupled to seagrass photosynthesis (Fig. 3; see also Section III). In addition, bacterial $\delta^{13}C$ ratios in sediment below the seagrass *P. oceanica* were similar to the seagrass $\delta^{13}C$ ratios suggesting that seagrass detritus and/or DOC released by the plant was the main carbon source for sediment microbial activity (Holmer et al., 2004).

Most of the research conducted on the effect of seagrass communities on DOC fluxes indicates that seagrass beds are net sources of DOC to the water column and the sediment. However, recently, it has been found that during colonization and development of a *C. nodosa* meadow, the seagrass community acts as net sink to DOC in the early stages, while it shifts to a net source of DOC in a mature bed (Barrón et al., 2004). Moreover, there is some recent evidence that seagrasses themselves may use DOC as carbon source, as occurs in terrestrial plants: terrestrial plants are able to use organic monomers released by microbial extracellular enzymes (Schimel and Bennett, 2004). Recently, Brun et al. (2003) cultured *Zostera noltii* with seawater enriched with $DO^{14}C$ released by *Ulva rigida*. The concentration of $DO^{14}C$ in the medium decreased while ^{14}C accumulated in the above- and below-ground tissues of the seagrass. Similar results were obtained in *Z. marina* by Smith and Penhale (1980). However, these experiments are not definitive, as some ^{14}C recovered in seagrass tissues could be incorporated as $^{14}CO_2$ after recycling of $DO^{14}C$ into $DI^{14}C$, and further investigations are needed to confirm the capacity of seagrasses to acquire DOC.

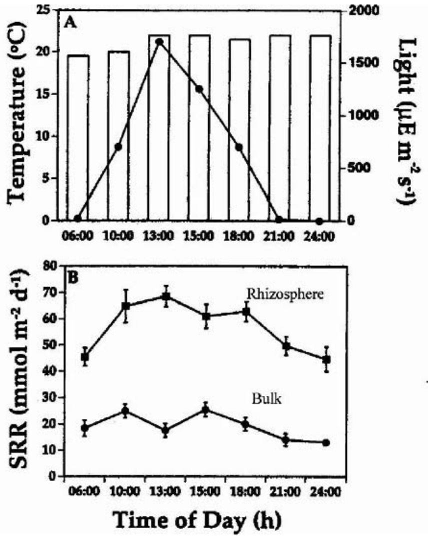

Fig. 3. Diel changes in temperature empty bars and light levels (dots upper panel) and sulfate reduction rates in rhizosphere and bulk sediment (lower panel) in a *Zostera noltii* seagrass bed, Arcachon, France. Sulfate reduction rates were stimulated during the day, where the seagrasses are expected to release photosynthetic products. Modified from Blaabjerg et al. (1998).

The release of DOM by seagrasses, to the water column and sediments, must play a major role in coastal biogeochemistry, since DOC increases bacterial activity and accelerates nutrient recycling and secondary production in coastal ecosystems. However, the significance of seagrass beds as sources of DOM for coastal biogeochemistry remains to be quantified for a larger number of seagrass species and locations. The DOC released by seagrass beds might also support open ocean production. The open ocean has been demonstrated to be heterotrophic (Duarte and Agustí, 1998; Duarte et al., 1999) and Arístegui et al. (2002) suggested that this carbon deficit could be supplied by DOC flux from coastal communities.

D. Dissolved Inorganic Carbon and Oxygen

Seagrass beds affect dissolved inorganic carbon (DIC) and dissolved oxygen (DO) concentrations in the coastal areas where they grow. Seagrass photosynthesis reduces the concentration of DIC in the water column and increases that of DO, while respiration increases DIC concentration at the expense of DO. This gas exchange has been extensively used as a physiological tool to estimate the primary production in seagrass itself (Zieman and Wetzel, 1980) and the community (Erftemeijer et al., 1993; see also Zimmerman et al., Chapter 13). A number of studies have shown that gaseous exchange across the leaf surface to the ambient seawater is restricted by the diffusive boundary layer (Larkum et al., Chapter 14) and have demonstrated transport of oxygen via the lacunae from the leaves to the underground organs (Pedersen et al., 1998; see also Borum et al., Chapter 10). The accumulation of respiratory carbon dioxide from internal recycling has also been indicated (Roberts and Moriarty, 1987). Thus, laboratory and *in situ* incubations or mass balances based on oxygen or DIC gas exchange in the water column have serious limitations in seagrass systems. Recent studies have pointed out the importance of taking into consideration the plant–sediment interactions in order to get a proper balance of the metabolic processes occurring in seagrass communities (Gacia et al., 2005). Indeed, the stoichiometric balance between oxygen production and DIC consumption deviates from the theoretical value (0.83; Oviatt et al., 1986) in studies of seagrass community metabolism (Ziegler and Benner, 1998; Barrón et al., unpublished data; Gacia et al., 2005). The dynamics of the carbonic–carbonate system (see Section II. E, this chapter), carbonate production and dissolution (see Section II. F, this chapter), anoxic mineralization with incomplete or partial oxidation in the sediment, and sulphate reduction processes (see Section III. E, this chapter) may interfere with the photosynthetic and respiratory balances of DO and DIC in the water column. More efforts should be made to quantify all these different potential interactions in order to fully evaluate the metabolism of seagrass communities based on photosynthetic gas exchange in the water column environment.

Seagrasses also directly influence oxygen concentration in sediment pore waters. A fraction of the O_2 transported to the rhizomes and roots, is released into the sediments (see Borum et al., Chapter 10); Pedersen et al. (1998) found an oxic microzone of about 80 μm around *C. rotundata* roots during light incubations. Similar findings have been reported for other seagrasses, e.g. *Z. marina* (Greve et al., 2003), *Halophila ovalis* (Connell et al., 1999) and could be a common feature of seagrasses (see also Kuo and den Hartog, Chapter 3). The transport of oxygen is most pronounced in the light, driven by photosynthesis in the leaves. However, the oxic microzone around *C. rotundata* roots was also present during dark incubations although then it diminished to 50 μm. It was shown that the oxygen present in the rhizosphere during darkness was supplied from the oxic water column to roots via gas-phase diffusion in leaves and rhizomes (Borum et al., Chapter 10). Pedersen et al. (1998) estimated that release of oxygen by roots contributed about 10% of the total sediment oxygen consumption. Oxygen supply by seagrass roots to the sediment has been recognized to be essential to maintaining non-toxic levels of sulfide for seagrass growth and survival (Pedersen et al., 1998; Eldrigde and Morse, 2000), whereas it would only partially support sediment aerobic bacterial metabolism (Pedersen et al., 1998; Eldrigde and Morse, 2000).

Seagrasses are highly productive plants but they also support a large biomass and production of animals and microbes, and a large respiratory activity partially dependent on the seagrass itself. To date, there are few estimates of the light compensation point for balanced metabolism (i.e. gross primary production = community respiration) in seagrass beds (Erftemeijer and Middelburg, 1993; D'Avanzo et al., 1996; Herzka and Dunton, 1997), but those available indicate very high light requirements for the whole ecosystem metabolism. Indeed, seagrass meadows may only be marginally autotrophic ecosystems (Hemminga and Duarte, 2000). Further work should extend the information on integrative studies of seagrass metabolism and its implications for the balance between aerobic and anaerobic processes in the whole coastal systems. For instance, the metabolic activity of *P. oceanica* beds has been shown to influence the concentration of oxygen and dissolved inorganic carbon in the water column within an entire Mediterranean bay partially colonized by seagrasses (Frankignoulle et al., 1984).

E. CO_2–Carbonate System and pH

Carbon dioxide and pH are closely linked in the marine environment through the photosynthetic activity of primary producers, such as seagrasses. Photosynthetic uptake of dissolved inorganic carbon results in a displacement of the CO_2/bicarbonate/carbonate balance from equilibrium:

$$\begin{aligned} &CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \\ &\quad \leftrightarrow CO_3^{2-} + 2H^+ \end{aligned}$$

decreasing the concentration of CO_2 and increasing that of HCO_3^- and/or CO_3^{2-}. These changes are coupled to water column pH fluctuations of low amplitude due to the buffering capacity of marine waters. However, in seagrass meadows with high biomass and productivity, significant daily fluctuations of pH, carbon dioxide, and dissolved oxygen are found coupled to the photosynthetic activity of the plants. In the NW-Mediterranean diel pH fluctuations of up to 0.5 units have been described just above and within

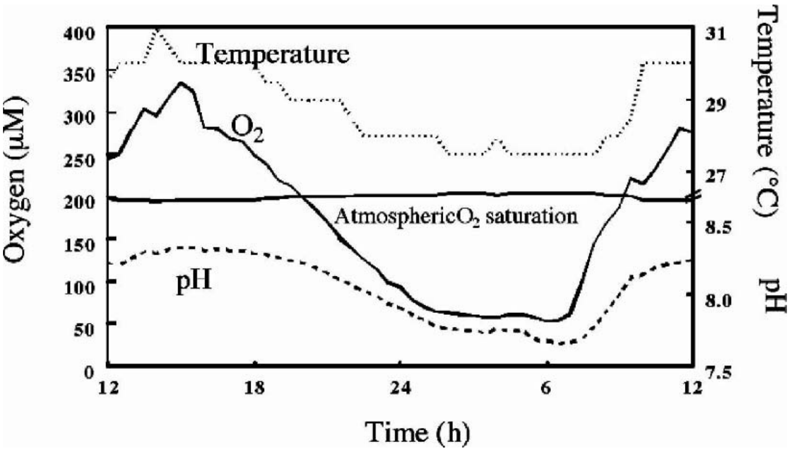

Fig. 4. Temperature, pH, and concentration of oxygen in the water column of Silaqui (The Philippines) during a daily cycle from the 28 to the 29 of March 2000 (Pedersen, unpublished data).

the leaf canopy of a shallow *C. nodosa* meadow. Similar pH amplitude changes were recorded in a shallow mixed seagrass meadow in the Philippines (Fig. 4). Hence, diel changes in pH within seagrass canopies indicate changes in metabolic activity of the meadow (including photosynthesis and respiration of seagrass and associated biota, and sediment metabolism).

The primary form of dissolved inorganic carbon in the marine environment is bicarbonate (90%), while carbon dioxide represents a minor fraction (0.5–1%) for seawater at pH 8.1–8.3 (and less than 0.1% at the higher range of pH as measured in the studies mentioned above). Seagrass photosynthesis, particularly in shallow and confined environments, is thus constrained by low CO_2 concentration and low molecular diffusion associated with the boundary layer around the leaves (see Koch et al.,Chapter 8 and Larkum et al., Chapter 14). To overcome such limitations most seagrass species are able to utilize HCO_3^- as a source of inorganic carbon for photosynthesis (James and Larkum, 1996; Beer and Rehnberg, 1997; Bjork et al., 1997; Invers et al., 1997; Swarz et al., 2000; see Larkum et al., Chapter 14), although less efficiently than CO_2.

Species-specific differences in the uptake kinetics of the different forms of DIC have been linked to the autoecology of different seagrasses. For instance, photosynthesis of *Z. noltii* living in a very shallow sheltered bay was less sensitive to pH increases than *C. nodosa* and *P. oceanica* from deeper and more open areas (Invers et al., 1997). Similarly, *Z. marina* and *Phyllospadix torreyi* from the Pacific showed less efficient bicarbonate usage than Mediterranean *C. nodosa* and *P. oceanica* which are exposed to higher irradiation and less water exchange due to the lack of tides (Invers et al., 2001). Also, intraspecific differences in the photosynthetic efficiency at high pH have been found between intertidal and subtidal forms of *C. serrulata* and *Halophila ovalis* in Zanzibar (Swarz et al., 2000), the intertidal forms being more exposed to wide pH fluctuations and more efficient in the bicarbonate use (see Larkum et al.,Chapter 14 for the physiological mechanisms involved in the uptake efficiency of the different forms of DIC at different pH's).

F. Carbonate Dissolution and Production in Seagrass Beds

In carbonate environments, the discrepancy mentioned in Section II.D between estimates of net primary production in seagrass communities using O_2 and DIC fluxes partially reflects the metabolism of carbonate in seagrass meadows (Eldridge and Morse, 2000; Burdige and Zimmerman, 2002). Dissolution of calcium carbonate ($CaCO_3$) consumes CO_2 from water column and pore water, and production of $CaCO_3$ releases CO_2, according to the equation:

$$CaCO_3 + CO_2 + H_2O \leftrightarrow Ca^{2+} + 2HCO_3^-$$

Dissolution of $CaCO_3$ in marine environments, however, only consumes 0.6 mol of CO_2 (Frankignoulle et al., 1984).

Seagrass beds affect the metabolism of $CaCO_3$ by enhancing (i) carbonate dissolution in the sediments and (ii) carbonate precipitation by associated epibionts. The effect of seagrass beds on deposition of organic matter, and the release of O_2 by seagrass roots and rhizomes into the sediments, enhances aerobic mineralization of organic matter, and, thus, generation of CO_2 available for carbonate dissolution in the sediments colonized. Recent studies (Eldridge and Morse, 2000; Burdige and Zimmerman, 2002) demonstrate that the high levels of organic matter decomposition occurring in seagrass sediments cannot be explained solely by the high concentration of DIC found in meadow pore waters. In addition, the excess of DIC in seagrass pore water observed cannot result from mineralization of organic matter by sulfate reduction, since sulfate reduction rates in seagrass carbonate sediments are low (e.g. Eldridge and Morse, 2000; Burdige and Zimmerman, 2002; Holmer et al., 2003). Using a diagenic model to explain the sediment profiles of concentrations of DOM, DIC, O_2, nitrate, ammonium, and sulfide in seagrass sediments from Laguna Madre, and considering O_2 release by seagrass roots, Eldridge and Morse (2000) showed that carbonate dissolution should contribute more than 50% to the pore water DIC concentration during early diagenesis in vegetated sediments. Burdige and Zimmerman (2002) obtained similar results by examining vertical pore water profiles of alkalinity, total DIC, Ca^{2+}, sulfide and pH in seagrass and bare sediments in Bahamas. They estimated that carbonate dissolution in shallow tropical sediments mostly colonized by *T. testudinum* would occur at rates ranging from 4 to 11 mmol $Ca_2CO_3 m^{-2} d^{-1}$, tending to increase with increasing shoot density. In addition, the observed rates of carbonate dissolution in the Bahamas seagrass sediments should consume about twice the amount of CO_2 produced by aerobic respiration if O_2 only was supplied by physical processes such as diffusion, bioturbation, and pore water advection (Burdige and Zimmerman, 2002). The rates of carbonate dissolution observed in seagrass sediments could only be explained if part of sediment aerobic respiration was driven by photosynthetically-derived O_2, released by seagrass roots (Burdige and Zimmerman, 2002). The effect of seagrass beds on sediment carbonate dissolution should, in turn, increase phosphorus pore water concentration, since a significant fraction of the phosphorus in seagrass carbonate sediments is adsorbed to carbonate minerals and can become available to the plants by acid dissolution (Burdige and Zimmerman, 2002). Therefore, the enhancement of sediment carbonate dissolution by seagrasses can increase phosphorus availability for seagrass uptake, and, since this nutrient often limits seagrass growth in carbonate sediments (see Romero et al., Chapter 9), it may increase seagrass production.

Most epibiota associated with the seagrass canopy in carbonate environments comprise calcifying organisms (see Borowitzka et al., Chapter 19). In tropical seagrass beds, for instance, calcium carbonate accumulation on seagrass leaves ranged from 0.004 g $CaCO_3$ $leaf^{-1}$ (in *Halodule uninervis*) to 0.417 g $CaCO_3$ $leaf^{-1}$ (in *E. acoroides*, Gacia et al., 2003). The rate of calcium carbonate production has been quantified for temperate and tropical seagrass communities, and it varies from 0.05 g $CaCO_3 m^{-2} d^{-1}$ to 7.67 g $CaCO_3 m^{-2} d^{-1}$ (Table 1). The large differences in calcium carbonate production among seagrass beds have been attributed to the wide variability in seagrass production, but generally carbonate production increases with seagrass productivity (Gacia et al., 2003). The amount of calcium carbonate produced by seagrass communities may represent close to 35% of total calcium carbonate deposited in seagrass sediments in very productive meadows, such as those in the Philippines (Gacia et al., 2003). Conversely, the contribution of seagrass beds to deposition of calcium carbonate is negligible ($<0.5\%$) in beds of low productivity, or in areas with high calcium carbonate deposition from other sources (Gacia et al., 2003). These estimates, however, do not account for potential losses of seagrass biomass and associated minerals due to grazing or leaf breaking, nor for the losses of sediment material from resuspension, which may vary significantly among sites. Precipitation of $CaCO_3$ in seagrass beds would increase CO_2 concentration in the water column, and, hence, it would stimulate seagrass photosynthesis. Carbonate precipitation, therefore, might supply a significant fraction of inorganic carbon to support high seagrass productivity in carbonate environments.

Available estimates of carbonate dissolution (Burdige and Zimmerman, 2002) and production rates (Table 1) indicate that carbonate metabolism, indeed, may be an important source of inorganic carbon to support seagrass productivity. However, the lack of published studies comparing net primary production and net carbonate metabolism in seagrass

Table 1. Estimates of calcium carbonate production by seagrass beds. Compilation from Gacia et al. (2003).

Community	$CaCO_3$ production ($g\ m^{-2}\ d^{-1}$)	Location	Reference
Thalassia testudinum	0.49	Jamaica	Land (1970)
Thalassia testudinum	7.67	Barbados	Patriquin (1972)
Thalassia hemprichii	0.92–6.52	Papua New Guinea	Heijs (1984)
Cymodocea rotundata	1.77	Papua New Guinea	Heijs (1984)
Halodule uninervis	3.08	Papua New Guinea	Heijs (1984)
Syringodium isoetifolium	5.95	Papua New Guinea	Heijs (1984)
Mixed meadow	2.89	Papua New Guinea	Heijs (1984)
Amphibolis antarctica	0.14–0.96	W Australia	Walker and Woelkerling (1988)
Thalassia testudinum	0.77	Florida	Frankovich and Zieman (1994)
Thalassia testudinum	0.08–0.83	Florida	Nelsen and Ginsburg (1986)
Thalassia testudinum	0.15–2.85	Florida	Bosence (1989)
Mixed meadow	0.48–2.08	The Philippines	Gacia et al 2003
Enhalus acoroides-Cvmodocea rotundata	0.05	The Philippines	Gacia et al 2003
Thalassia hemprichii	0.38	Vietnam	Gacia et al 2003
Mixed meadow	0.52	Vietnam	Gacia et al 2003
Enhalus acoroides	0.12	Vietnam	Gacia et al 2003
Caulerpa prolifera-Cvmodocea nodosa	0.17	Spain	Canals and Ballesteros (1997)
Posidonia oceanica	0.19	Spain	Canals and Ballesteros (1997)
Posidonia oceanica	0.43	Spain	Romero (1986,1988)

communities does not allow quantification of the importance of carbonate metabolism for seagrass production in carbonate environments. In addition, extensive and highly productive seagrass beds growing in carbonate coastal areas with low sediment inputs from terrigenous sources might export significant amounts of calcium carbonate to maintain the sedimentary budget of adjacent beaches.

G. Redox Potential

The effects of seagrass beds on deposition of organic matter, the release of O_2 from seagrass roots, and stimulation of bacterial activity (see next section) in the colonized sediments have the potential to alter the overall biogeochemical conditions, and, thus, redox potential in the sediments. Seagrass meadows grow on sediments with redox potentials ranging from -175 to $+300$ mV (Terrados et al., 1999; Enríquez et al., 2001; Marbà and Duarte, 2001). Seagrass sediments tend to present redox potentials less negative than those in adjacent bare sediments, indicating that seagrass activity contributes to maintain more oxidizing sediments more suitable for plant growth and survival, especially in terms of sulfide levels. For instance, rhizospheres of *C. nodosa* (Marbà and Duarte, 2001), *T. testudinum* (Enriquez et al., 2001), and *Z. noltii* (Isaksen and Finster, 1996), respectively, present redox potentials 112, 211, and 189 mV higher, respectively, than adjacent unvegetated sediments. The capacity of seagrass meadows to oxidize sediments depends on plant photosynthetic activity, as demonstrated *in situ* by shading experiments: sediment redox conditions in a *T. testudinum* rhizosphere declined 45 mV when the meadow was exposed to 27% incident irradiance for 5 days (Enriquez et al., 2001). Similarly, redox potential in sediments colonized by a tropical mixed seagrass meadow declined by 108 and 226 mV when light availability for 6 days was 50% and 10% of incident irradiance, respectively (Gacia et al., 2005). In addition, the structure of seagrass rhizospheres constrains the magnitude of seagrass effects on sediment redox conditions, and most of the positive redox potential anomaly and rhizosphere biomass occur at similar sediment depths (Enriquez et al., 2001; Marbà and Duarte, 2001).

The effects of seagrass beds, in this way, may not always be positive. Development of a seagrass bed may enhance enrichment of sediment organic matter and seagrass community respiration, and thus community metabolism may become heterotrophic (e.g. Barrón et al., 2004). Under such conditions the sediments of seagrass bed are more anoxic than adjacent bare sites (Enriquez et al., 2001; Barrón et al., 2004). The effects of seagrass metabolism, bed structure, and the amount of organic matter in the sediment on sediment redox potential evidently combine in different ways to influence sediment redox conditions during seagrass meadow development. For instance, the greatest positive redox potential anomaly in sediments colonized by a deep loose *C. nodosa* meadow during the growing season occurred at the beginning of summer, when leaf biomass was highest and seagrass rhizosphere was not yet completely developed (Marbà and Duarte, 2001). Similarly, sediment redox conditions tended to be less positive the longer the time after *C. nodosa* colonization (Barrón et al., 2004).

Seagrass activity, therefore, is able to attenuate sediment anoxic conditions within the sediment layers occupied by seagrass rhizospheres. Changes in redox potential promoted by seagrasses are evident in sediments where seagrass roots are spaced by several centimeters (Marbà and Duarte, 2001), and, hence, at spatial scales larger than those where oxygen released by seagrass roots is detected with microelectrodes (80 μm; Borum et al., Chapter 10). Therefore, the effect of seagrasses on sediment redox properties should result from O_2 root release, and oxidation of reduced compounds (e.g. iron, sulphide) creating a suboxic zone.

III. Mineralization of Organic Matter and Nutrient Cycling in Seagrass Sediments

A. Microbial Activity

The decomposition of organic matter in seagrass sediments occurs through a consortium of microbial communities (Table 2). As oxygen penetration is generally limited to the upper few millimetres or centimetres of coastal sediments, the activities of anaerobic heterotrophic microbial communities are particularly important (Fenchel et al., 1998; Thamdrup, 2000). Via the microbial food chain, complex organic substrates are remineralized in several steps, as particulate organic carbon is solubilized to high molecular weight dissolved organic carbon, which is enzymatically hydrolyzed to lower molecular weight substrates (Fenchel et al., 1998). These lower molecular weight substrates are transformed into fermentation products such as volatile fatty acids, which are ultimately remineralized to CO_2. The pore water pools of dissolved organic compounds, such as DOC, volatile fatty acids, and dissolved carbohydrates in seagrass sediments are generally enhanced compared to unvegetated sites (Holmer and Nielsen, 1997; Burdige and Zimmerman, 2002) indicating that there is more substrate available for the bacteria in the rhizosphere sediments. A variety of electron acceptors can be used by microbial communities in the final steps of remineralization. In marine sediments, sulfate is quantitatively the most important electron acceptor under anoxic conditions (Jørgensen, 1982), but recent studies have demonstrated that microbial iron reduction and manganese reduction can also be important, in particular in sediments with high reoxidation capacities (Thamdrup, 2000). Denitrification supported by nitrate from the water column or through coupled nitrification–denitrification is also an important process for the nitrogen cycling in marine sediments, but due to the low carbon oxidation in this process, denitrification has a minor effect on the marine carbon cycle (Fenchel et al., 1998).

B. Nitrogen Cycling

Seagrasses can influence nitrogen cycling in sediments by several direct and indirect mechanisms. The production of ammonium through mineralization may be enhanced by (i) accumulation of allochthonous particulate organic material trapped within the meadows (Kemp et al., 1983), (ii) microbial breakdown of dissolved organic nitrogen released from plant roots (Smith et al., 1988), and (iii) decomposition of senescent plant material (Pedersen et al., 1999). The production of ammonium through mineralization is an important source of nitrogen for plant growth (Pedersen and Borum, 1992; Holmer et al., 2001), but nitrogen fixation also contributes significantly both to the nitrogen cycling in the sediments (Table 3) and to support plant growth. In tropical seagrass beds, sediment nitrogen fixation has been estimated to provide more than 50% of plant nitrogen demand (review by Welsh, 2000), whereas it tends to be much lower in temperate sediments, usually less than 12% (review by Welsh, 2000) or even $<5\%$ as found for a *Z. marina* community in Denmark (McGlathery et al., 1998). Studies have demonstrated a coupling between nitrogen fixation and the photosynthetic activity of the plants via the exudation of fixed carbon by the root system (Welsh, 2000). Nielsen et al. (2001) found that about one-third of the nitrogen fixation activity in the rhizosphere sediment was directly associated with the

Table 2. Conceptual presentation of the mineralization processes in marine sediments showing the different electron acceptors used for organic matter (CH_2O) oxidation (after Canfield et al., 1993). Nitrification is also shown for completeness. For simplicity the equations are not balanced.

O_2 respiration	$CH_2O + O_2 \rightarrow CO_2 + H_2O$
Nitrification	$NH_4^+ + O_2 \rightarrow NO_3^- + H_2O + H^+$
Denitrification	$CH_2O + NO_3^- + H^+ \rightarrow CO_2 + N_2 + H_2O$
Manganese reduction	$CH_2O + MnO_2 + H^+ \rightarrow CO_2 + Mn^{2+} + H_2O$
Iron reduction	$CH_2O + FeOOH + H^+ \rightarrow CO_2 + Fe^{2+} + H_2O$
Sulfate reduction	$CH_2O + SO_4^{2-} + H^+ \rightarrow CO_2 + H_2S + H_2O$
Methanogenesis	$CH_2O \rightarrow CO_2 + CH_4$

roots and rhizomes, suggesting that nitrogen fixing bacteria colonized the roots. They were not able to identify the bacteria, but high sulfate reduction activity suggests that sulfate-reducing bacteria were responsible for the nitrogen fixing (Welsh et al., 1996; Küsel et al., 1999; Welsh, 2000). The linkage between nitrogen fixation and sulfate reduction needs further investigation to fully explore the suggested benefits for the seagrasses.

C. Nitrification and Denitrification

The effect of seagrasses on nitrification and denitrification processes has been under intense investigation (Table 3), in particular in meadows affected by eutrophication, where it is essential to know the potential for nitrogen removal through denitrification (Borum and Sand-Jensen, 1996). Nitrification is controlled primarily by O_2 and nitrogen as ammonium supply, while denitrification is controlled by nitrate and organic carbon supply. Often these two processes are closely coupled in time and space through nitrification–denitrification. The results on rates of nitrification and denitrification coupled to nitrification in rhizosphere sediments are inconsistent, since some workers (Iizumi et al., 1980; Caffrey and Kemp, 1990; Shieh and Yang, 1997) report high rates, whereas other recent studies using the ^{15}N-isotope pairing technique, report low rates of nitrification and denitrification (Risgaard-Petersen et al., 1998; Rysgaard et al., 1996; Ottosen et al., 1999, Welsh et al., 2000). High rates are associated with release of oxygen from the roots, whereas studies where low rates are measured indicate a strong competition between nitrifying bacteria and seagrass roots for ammonium, which eventually decreases the coupled nitrification–denitrification (Welsh et al., 2000). These findings suggest that the effect of seagrasses on the removal of nitrogen from the marine ecosystem is species-dependent, where some species increase the removal and others reduce the removal compared to unvegetated sites. Due to the large seasonal variation in modifying factors, such as the oxidation of the sediments and the nutrient uptake by the plants, a large seasonal variation in the importance of denitrification can be expected. So far, seasonal studies have focused on *Zostera* spp., where the denitrification was low (Risgaard-Pedersen and Ottosen, 2000), whereas larger species, with more below-ground biomass, remain to be examined. Also diel changes in pore water ammonium pools and denitrification rates have been reported in *H. beaudetti* meadows, with high dawn ammonium pools and denitrification rates declining during the day, indicating that nitrogen assimilation by the plant roots regulates pore water ammonium pools and thus, indirectly, rates of nitrification and denitrification in the rhizosphere (Blackburn et al., 1994). Further studies are needed to quantify the importance of diel changes for nitrogen cycling in seagrass meadows.

D. Iron Cycling

Microbial iron reduction is an important mineralization process in sediments with high iron concentrations such as in terrigenic sediments. A positive correlation between pools of oxidized iron and microbial reduction rates has been found to apply in all studies so far (Thamdrup, 2000). There are no reports on iron reduction activities in seagrass sediments, but visual observations of rhizosphere sediments from a range of seagrass species extending from temperate terrigenic to tropical carbonate beds

Table 3. Process rates in seagrass sediments. Values for unvegetated sediments are given in parentheses.

Seagrass species	Location	Nitrification µmol N $m^{-2}h^{-1}$	Denitrification µmol N $m^{-2}h^{-1}$	N_2 fixation µmol N $m^{-2}h^{-1}$	Sulfate reduction mmol $m^{-2}d^{-1}$	References
Temperate						
Cymodocea nodosa					21 (18)	Holmer (unpublished)
Posidonia oceanica	Spain				3–12 (1–11)	Holmer et al. (2003)
Zostera marina	USA	410–2481 (228–2273)	71–209 (10–67)			Caffrey and Kemp (1990)
	Denmark		17	8–18		Risgaard-Petersen et al. (1998)
	Denmark		1.5			Ottosen et al. (1999)
	Denmark					Risgaard-Petersen et al. (2000)
	Denmark			3.5–17.8		McGlathery et al. (1998)
	Denmark				25–59.1 (12.2)	Holmer and Nielsen (1997)
	Denmark				13.2–29.6 (7.8–22.1)	Boschker et al. (2000)
	Netherlands				7.4 (2.4)	Boschker et al. (2000)
	Denmark				12–70	Blaabjerg et al. (1998)
	Denmark				19–41	Holmer and Laursen (2002)
Zostera noltii	France					Rysgaard et al. (1996)
	France					
Inner eutrophic station			3–12			Wit et al. (2001)
	France outer station			5–29		Wit et al. (2001)
	France		2–6	15–19	13.7	Welsh et al. (1996, 2000)
	France				29 (14.6)	Isaksen and Finster (1996)
Tropical/ subtropical						
Cymodocea rotundata	Thailand				6(2)	Holmer et al. (2001)
Enhalus acoroides	Australia			74		Moriarty and O'Donohue (1993)
	Australia				90(12)	Pollard and Moriarty (1991)
	Thailand				6–21	Holmer et al. (1999)
Halodule beaudetti	Jamaica			83	34	Blackburn et al. (1994)
Syringodium isoetifolium	Australia			48–140		Moriarty and O'Donohue (1993)
Thalassia hemprichii	Australia			39–56		Moriarty and O'Donohue (1993)
	Thailand				2 (2)	Holmer et al. (2001)
Thalassia testudinum	USA				5	Ku et al. (1999)
Zostera capricorni	Australia			57–69		Odonohue et al. (1991)
	Australia					Hansen et al. (2000)

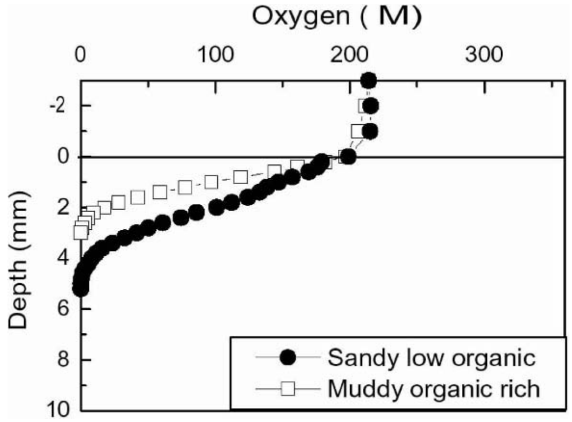

Fig. 5. Oxygen penetration depth in two *Posidonia oceanica* meadows in the Cabrera National Parc, Mallorca Island. The oxygen profiles were measured by use of oxygen microsensors during the summer (June 2001) with high productivity in the meadows. One site was characterized as pristine with low-organic (0.5 %OC) sandy carbonate sediments, whereas the second site was enriched by organic inputs from visiting boats and enhanced primary productivity at the location. These sediments were organic enriched (2.6 %OC). Redrawn from Holmer et al. (2003).

indicate that oxidized iron concentrations are probably low since there are no signs of oxidized iron by coloration of the roots, rhizomes, and sediments, as has been found for freshwater macrophytes (Christensen et al., 1998).

Elevated iron pools in the rhizosphere of salt marsh sediments have been shown to be associated with suppressed sulfate reduction (Gribsholt et al., 2003): sulfate reduction was almost absent in the rhizosphere of *Spartina alterniflora*, whereas iron reduction accounted for >99% of the carbon oxidation and it was among the highest reported rates for marine sediments (Gribsholt et al., 2003). Iron pools are very low in carbonate seagrass sediments (Berner, 1984; Chambers et al., 2001; Holmer et al., 2003), and although the oxidation of the sediments is relatively high compared to unvegetated sites, suggesting that iron can be rapidly regenerated, it is not likely that iron reduction is an important mineralization process. Redox potentials are generally low compared to terrigenic oxidized sediments and examination of carbonate sediments in *P. oceanica* meadows also show that the oxygen penetration depth is low (Fig. 5), and high rates of sulfate reduction have been found close to the sediment surface suggesting that iron is consumed through reoxidation of sulfides rather than by microbial respiration (Holmer et al., 2003).

E. Sulfur Cycling

Knowledge on sulfur cycling in seagrass sediments has grown significantly during the last decade, and sulfate reduction rates have generally been found to be stimulated by seagrasses compared to unvegetated sediments (Table 3; Isaksen et al., 1996; Holmer and Nielsen, 1997; Nielsen et al., 2001; Holmer et al., 2003). Sulfate reduction is an important mineralization process in marine sediments due to high sulfate concentrations in seawater; and pools of other electron acceptors appear to be reduced in seagrass sediments due to competition from the plants (nitrogen) or due to the strongly reducing conditions as a result of the high respiratory activity (plants and microbes). Sulfate reduction is probably stimulated for the same reasons as mentioned for nitrogen: increased input of allochthonous material, decomposition of senescent plant material, and release of organic compounds from the roots. Sulfate reduction rates have been found to be stimulated during the day with active photosynthesis (Fig. 3), and additions of sugars to rhizosphere sediments enhance sulfate reduction activity suggesting that the organic matter is released from the roots (Blaabjerg and Finster, 1998; Blaabjerg et al., 1998; Nielsen et al., 2001). Positive correlation between sulfate reduction rates and below-ground biomass also suggest that the activity is associated with the presence of the seagrasses (Isaksen and Finster, 1996; Holmer and Nielsen, 1997; Blaabjerg and Finster, 1998; Blaabjerg et al., 1998). The effect of roots on sulfate reduction rates may, however, turn out to differ significantly among seagrass species, as recent results with *Posidonia oceanica* show a negative correlation between the root biomass and sulfate reduction rates (Holmer et al., 2003). Sulfate reduction rates were significantly higher compared to unvegetated sites, but decreased with increasing root biomass. This suggests that the roots control the sulfate reduction rates, e.g. by creating a more oxidized environment and favoring other mineralization processes.

High rates of sulfate reduction may lead to high concentrations of sulfide in pore waters, in particular if the sulfide buffering capacity of the sediments is low. The sulfide buffering capacity is defined as the sediments capacity to reoxidize and thereby detoxify the sulfides. The reoxidation capacity is primarily determined from the pools of oxidized iron, but also regeneration of this pool, e.g. through bioturbation or diffusion of oxygen from the water column to the sediments. Sulfide is considered to be a phytotoxin as it interferes with cytochromes in the electron transfer chain in the plants and thus affects the energy balance of the plants (Erskine and Koch, 2000; Koch et al., Chapter 8). A negative energy balance may eventually lead to increased mortality in the meadows. High concentrations of sulfides have been suggested to be responsible for large die-back events, in particular in carbonate sediments with low buffering capacity – due to low pools of oxidized iron (Barber and Carlson, 1993; Carlson et al., 1994). Experimental studies with additions of sugar to the sediments to enhance anoxia and sulfide concentrations are consistent with these observations; Terrados et al. (1999) found reduced leaf growth and increased mortality in tropical species growing on carbonate sediments such as *T. hemprichii*, whereas temperate species growing on terrigenic sediments such as *C. nodosa* and *Z. marina* showed only a minor response. Recent studies on carbonate sediments, however, show that some seagrasses such as *T. testudinum* which have been subjected to die-back events (Carlson et al., 1994) are quite sulfide tolerant and only long-term exposures to high concentrations lead to significant die-back (Erskine and Koch, 2000). One possible explanation for this observation may be found in the diurnal changes in sulfide concentrations in rhizosphere sediments of *T. testudinum*. Lower concentrations during the day (Lee and Dunton, 2000) suggest that the sulfide exposure is less during the day due to photosynthetically-driven release of oxygen from the roots (Section II.D).

The finding by Pedersen et al. (1998) of an oxic microzone around the roots also during the night suggests that some seagrasses tranport oxygen out of the roots even in the dark and that these plants are exposed to high sulfide concentrations only under extreme conditions, e.g. if the sulfide production in the sediments is unusually high and exceeds the oxidation capacity from the root related oxygen translocation. Sulfide concentrations may also increase during night if oxygen is depleted in the water column due to high respiratory activity in the seagrass meadow or during calm wind conditions with low water exchange. If no oxygen is present in the water column the oxygen translocation to the roots will be limited to the active photosynthetic period. *Z. marina* was found to die during prolonged exposure to low oxygen concentrations in the water column, and the die-back was of similar magnitude as exposure to water column sulfide suggesting that anoxia was just as critical as the presence of sulfide (Holmer and Bondgaard, 2001). This is consistent with findings by Greve et al. (2003) that anoxic conditions around *Z. marina* plant leads to degradation of cells in the meristematic region and plant death. The die-off is exaggerated as water temperature increases suggesting that a number of factors may contribute to the die-back events observed in nature.

During anoxic conditions sulfide has been found inside the meristematic region of *T. testudinum*, and this had an immediate detrimental effect on the seagrasses (Borum et al., Chapter 10). The plants were only able to survive if sulfide was rapidly reoxidized, e.g. by onset of photosynthesis by dawn. This suggests that seagrasses are able to survive short periods of sulfide exposure as long as oxygen is present in the water column or is produced by the plant itself. A study with *Zostera marina* shows, that the intruding sulfides are reoxidized to elemental sulfur in the below-ground tissues, where it accumulates to high concentrations (Fig. 6). This may be an important mechanism for detoxification of the intruding sulfides and for avoiding sulfide exposure in the more

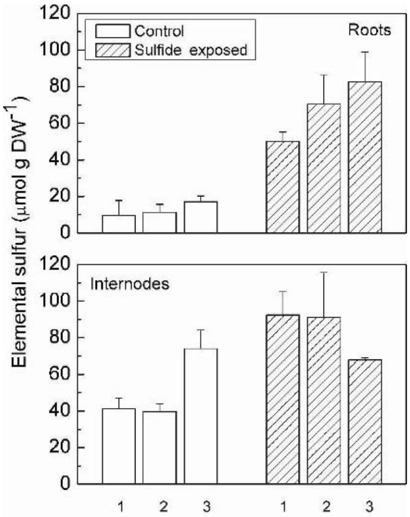

Fig. 6. Accumulation of elemental sulfur in *Zostera marina* roots (upper panel) and internodes (lower panel). *Z. marina* was grown in the laboratory for 3 weeks in a sandy sediment (Control) and in a sandy sediment amended with high concentrations of glucose to stimulate sulfide concentrations in the sediments (Sulfide exposed). Elemental sulfur was extracted from the 3 youngest roots and internodes (no. 1–3) and the concentrations were highest in the sulfide exposed internodes and decreased from the youngest to the oldest compartment. Modified from Holmer et al. (in press).

sensitive parts of the seagrasses, such as the meristematic region. The degree of detoxification in *Z. marina* was dependent on the reoxidation capacity of the plants, as shaded plants with reduced photosynthetic activity showed clear signs of sulfide exposure with rotting meristems (Holmer, unpublished data).

During eutrophication the anaerobic decomposition of organic matter increases, and sulfate reduction may increase further in the seagrass sediments. The organic enrichment of *P. oceanica* sediments observed toward marine fish farms is coupled to increasing sulfate reduction rates (Holmer, unpublished data). As seagrasses also may suffer from reduced light conditions in the water column due to blooms of phytoplankton and increased growth of epiphytes caused by eutrophication (Borum and Sand-Jensen, 1996) sulfide stress may add to reduced performance of the seagrass meadows.

F. Interactions Between Iron and Sulfur Cycling

Recent studies have investigated the importance of iron pools in carbonate sediments as a buffer against sulfide toxicity. Iron additions to *T. testudinum* growing on carbonate sediments resulted in increased above-ground biomass and it was suggested that decrease of sulfide levels due to enhanced precipitation of iron-sulfides, and thus detoxification, improved plant performance (Chambers et al., 2001). Iron additions have also been made to organic-enriched carbonate sediments with the slow-growing seagrass *P. oceanica* (Holmer et al., in press). Here it was found that, in addition to the improved sediment conditions, the availability of iron also increased, and the activity of the iron-demanding alkaline phosphatase enzyme increased. The uptake of phosphate was stimulated and seagrass growth increased. This is consistent with previous findings of iron deficiency in seagrasses growing in carbonate sediments (Duarte et al., 1995).

Iron concentrations are generally higher in fine-grained terrigenic sediments, which increase the potential for reoxidation of sulfides by oxidized iron as well as burial of sulfides as iron-sulfides or pyrites (FeS_2). The reoxidation of sulfide is complex and often involves many different processes, of both chemical and biological origin. Sulfate is the most important end-product of reoxidation and can be utilized again by sulfate reducing bacteria. Reoxidation is an important process as $>90\%$ of the sulfide production is considered to be reoxidized (Thode-Andersen and Jørgensen, 1989), and it may be even higher in seagrass sediments due to the release of oxygen from the plant roots. The burial of sulfides in marine sediments is thus minor compared to the production, and is often positively correlated to the sulfate reduction activity. The enhanced sulfate reduction activity found in seagrass sediments is also reflected in increased burial of reduced sulfides compared to unvegetated sediments in both terrigenic and carbonate sediments (Holmer and Nielsen, 1997; Holmer and Laursen, 2002; Holmer et al., 2003). Enhanced precipitation of sulfides with iron in carbonate sediments, e.g. due to eutrophication, may increase the iron deficiency of the seagrasses. Pools of sulfides have also been shown to be positively correlated with the shoot density and biomass (Holmer and Nielsen, 1997) and the burial of sulfides thus increases during seagrass colonization. For carbonate sediments, where the iron availability is limited, this scenario may lead to iron deficiency and lowered sulfide buffer capacity. Eventually this may limit the colonization of the seagrass meadows.

G. Phosphorous Cycling and Interactions with Iron and Sulfur Cycling

The cycling of phosphorus in seagrass beds has been examined indirectly by measuring phosphorus contents of seagrass tissues to assess nutrient limitation (Duarte, 1990; Fourqurean and Zieman, 2002), whereas the dynamic interactions between nutrient uptake and phosphorus availability in the water column and sediments remain to be examined. Phosphorus limitation is thought to control seagrass growth in carbonate sediments, although it has been shown that the sedimentary pools of phosphorus can potentially support plant growth for decades (Jensen et al., 1998). The phosphorus appears to be almost irreversibly bound in organic and carbonate pools (Jensen et al., 1998), despite a small fraction of it becoming available in pore waters as a result of enhanced carbonate dissolution by seagrass beds (Burdige and Zimmerman, 2002; see also Section II.F, this Chapter). The dissolution of inorganic pools and mineralization of organic pools is too slow to support maximum seagrass growth rates, and the pore water pools only represent a small fraction of the required nutrients (McGlathery et al., 2001). Fertilization studies have shown that seagrass growth and patch expansion are enhanced by additions of phosphorus rather than nitrogen to carbonate sediments confirming the significance of sedimentary pools for seagrass growth and phosphorus as an important limiting nutrient in carbonate sediments (Udy et al., 1999; Jensen and Bell, 2001). A study, in the tropical seagrass, *Cymodocea rotundata,* showed that mineralization of organic matter is important in sustaining seagrass growth, since the regenerated nutrients supported up to 81% of the phosphorus incorporation (Holmer et al., 2001).

Terrigenic seagrass sediments generally have higher phosphorus pools, where phosphorus is bound either in organic matter or in mineral pools and pore water only represents a minor pool, (Pedersen et al., 1997; Perez et al., 2001; Wit et al., 2001). The mineral-bound pools are redox sensitive, as phosphate is bound to oxidized iron (Jensen et al., 1995; Azzoni et al., 2001; Wit et al., 2001), and oxidized iron concentrations may show large seasonal fluctuations due to high microbial reducing activity in summer. In eutrophic sediments vegetated with *Ruppia cirrhosa* (Azzoni et al., 2001) the seasonal changes in iron-bound, exchangeable and pore water phosphate pools were, however, quantitatively of minor importance due to small pool sizes and very low concentrations of labile oxidized iron in the sediments. In eutrophic sediments sulfides compete with phosphate for oxidized iron, lowering the overall availability of oxidized iron (Thamdrup, 2000).

Seagrass beds are generally considered to act as sinks of phosphorus, which to a large degree can be considered to be recycled within the beds during colonization and development (Pedersen et al., 1997). Only under eutrophic conditions have seagrass beds been shown to act as sources of phosphorus to the surrounding environment, as found for *C. nodosa* in the Mediterranean (Perez et al., 2001). Under hypertrophic conditions in a *Ruppia maritima* meadow sulfate reduction was found to increase and compete with phosphate for oxidized iron. As a result phosphate was released from the sediments and eutrophication was increased even further and the seagrass eventually disappeared (Heijs et al., 2000). This is an excellent example of the complex interactions between P, Fe, and S in the marine environment.

IV. Summary and Future Work/Outlook

The studies of seagrasses during the past two decades clearly show the influence of seagrasses on sediment biogeochemistry and vice versa. Seagrass beds modify chemical conditions (concentration of organic matter, carbonates, O_2, DIC and nutrients, and pH) in the water column and the sediments of the coastal zone (Fig. 7), including the immediate colonized areas and, to some extent, adjacent systems. The chemical changes promoted by seagrass beds constrain microbial processes such as nitrogen fixation and mineralization of organic matter in seagrass sediments (Fig. 7), which, in turn, modify the chemical conditions of the bed environment through their end products (e.g. nutrients, CO_2, H_2S, see Fig. 7). Seagrass beds, therefore, play an engineering role (*sensu* Jones et al., 1997) in coastal biogeochemistry, affecting, for instance, carbon, nitrogen, and sulfur cycles (see also Mateo et al., Chapter 7; Romero et al., Chapter 9).

The effects of seagrass beds on coastal biogeochemistry are, however, species specific. Some seagrasses, such as those with low below-ground biomass only have minor effect on the sediment processes (e.g. *Z. marina* at nutrient-rich locations, where the below-ground biomass is low), whereas others with large below-ground biomass may alter the processes significantly compared to unvegetated sediments (e.g. *P. oceanica* in oligotrophic sediments). Also seasonal effects have a major influence on sediment biogeochemistry, e.g. the large seasonal variation found in redox potentials in rhizosphere sediments of *C. nodosa*; however, this has only been described so far for a few species, at a few locations and for a limited array of biogeochemical processes. Another example is the nitrogen cycling in the seagrass meadows, which primarily has been studied for seagrasses like *Zostera spp*, and where very little is known for larger and slow-growing species. Due to divergent results obtained with established methods, it will be important in future to include methodological studies, probably with ^{15}N, as this approach is suitable for use at community level for both field and experimental studies. Studies of seagrass meadows at the community level are greatly needed, as seagrasses seldom show the same growth pattern in small micro/mesocosms compared to the field. For the nitrogen cycling there is also a challenge to quantify nitrogen fixation and investigate the microbial ecology for more seagrass species, and under various growth conditions to understand the nutrient cycling in seagrass beds.

The type of sediment substrate is of major importance in understanding the effect of seagrasses on sediment biogeochemistry. There is a major

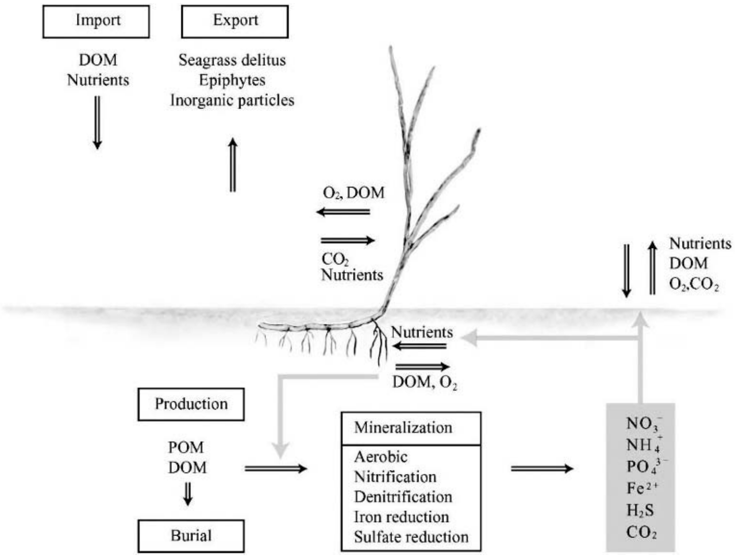

Fig. 7. Conceptual model of seagrass-water column and sediment interactions.

difference between terrigenic and carbonate sediments for a number of important elements such as P, Fe, and S. One example is the high concentration of sulfides in carbonate sediments found during die-back events, but also the cycling of P is strongly related to the sediment composition. In terrigenic sediments P dynamics are correlated with contents of oxidized iron, whereas they are influenced by the carbonates in the biogenic sediments. A focus on interactions between P, Fe, and S is needed to improve our understanding of phosphorus and iron limitation in seagrass beds, and the complex effects of sulfides.

Seagrass beds are highly dynamic systems, exhibiting large temporal changes in their structure (Walker et al., Chapter 23). The effects of seagrass beds on coastal biogeochemistry should, thus, change during their life-span. The influence of seagrass beds on coastal biogeochemistry appears to increase as seagrass colonization proceeds; limited evidence, based on *Cymodocea nodosa* colonization, suggests that mature beds, enhance seagrass production (Cebrián et al., 2000), leaf decomposition (Cebrián et al., 2000), burial of organic matter (Pedersen et al., 1997), and availability of N and P in the sediments colonized (Pedersen et al., 1997). The interactions between seagrass beds and biogeochemical processes, however, may result in deleterious conditions for the plant in advanced stages of the colonization process, if seagrass community metabolism results in heterotrophy and the amount of oxygen translocated to the rhizosphere is not enough to prevent plant exposure to high sulfide concentrations in the sediment. Increase in export of production from seagrass beds during the colonization sequence (Cebrián et al., 2000, Barrón et al., 2004) may be a mechanism to prevent seagrass beds developing a self-poisoning environment.

Although seagrass beds are in rapid decline in many coastal zones world-wide, little research has been undertaken to explore the changes on coastal biogeochemistry during meadow decline. The wasting disease in Northern America and Northern Europe during the 1930s resulted in significant coastal erosion and loss of fisheries habitat, but as eelgrass is a fast-growing species with rapid colonization capacity most of the eelgrass meadows were re-established within 10 years. It has turned out to be much more difficult to assess the effects of eutrophication and recession of depth limits for eelgrass, as the coastal ecosystems appear to change in multiple directions. Effects of eutrophication may be severe for slow-growing species such as *P. oceanica* in the Mediterranean due to low re-colonization capacity. High loading of organic matter in seagrass meadows, e.g. due to fish farming, has shown unbalanced metabolism leading to strong heterotrophy, loss of seagrass biodiversity, overgrowth of epiphytes, and macroalgae and increased seagrass mortality, conditons which persist for years after cessation of the impacting activities (e.g. Delgado et al., 1999). The mechanisms behind seagrass decline and its effects on coastal biogeochemistry remain a challenge for future seagrass studies.

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Chapter 7

Carbon Flux in Seagrass Ecosystems

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I. Introduction

Understanding matter circulation in the biosphere constitutes one of the fundamental research objectives for ecologists. Stocks of materials, their distribution, and their fluxes between different compartments are basic parameters that need to be characterized to explain the functioning of any ecosystem. Their study is usually arduous owing to the variety of routes that materials can follow, and to the complexity of the processes that are involved. Leopold (1949) described matter flux in ecosystems in a brief but elegant way in what he named '*The odyssey of the atom X*': "*An atom at large in the biota is too free to know freedom; an atom back to the sea has forgotten it. For every atom lost to the sea, the prairie pulls another one out of the decaying rocks. The only certain truth is that its creatures must suck hard, live fast, and die often, lest its losses exceed its gains*." When an atom abandons its long rest in the lithosphere and joins the organic compartment of the biosphere, it enters in that fast cyclic dynamic that characterizes life. Autotrophic organisms bring an atom to life, while the organism's death leaves it at the mercy of decomposers that return it to the inorganic compartment where it waits to join a new cycle. The persistence of an ecosystem relies on both the optimization of carbon and nutrient acquisition and on the minimization of carbon and nutrient losses (Hemminga et al., 1991). In other words, persistence requires a continuous effort to prevent the atoms essential for life from escaping the fast cycles that enable the high production we observe on our planet. Therefore, a fine tuned balance between production and remineralization (and the fluxes between sources and sinks) govern the rhythm of the ecosystems.

This chapter, far from pretending to be an exhaustive examination or reassessment of what is known about carbon fluxes in seagrass ecosystems, is an attempt to put a picture of carbon flux in focus by combining equal parts of literature review, personal achievements (including some recent unpublished and submitted results), a critical appraisal, and

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Table 1. Comparison between average seagrass and other marine and terrestrial ecosystems. NPP (net primary production). Simplified and modified from Margalef, 1986 and Duarte and Cebrián, 1996.

System	Area covered (10^6 km^2)	NPP (gC m^{-2} year^{-1})	Total NPP (PgC year^{-1})
Marine phytoplankton			
Oceanic waters	332	130	43
Coastal waters	27	167	4.5
Coastal macrophytes			
Mangroves	1.1	1000	1.1
Seagrasses	0.6	817	0.49
Macroalgae	6.8	375	2.55
Microphytobenthos	6.8	50	0.34
Terrestrial ecosystems			
Forests	41	400	16.4
Crops	15	350	5.25
Deserts	40	50	2
Terrestrial ecosystems	148	200	29.6
Continental waters	1.9	100	0.19
Oceans	359	132	47.5

thought-provoking estimates. Our goal is to provide a critical summary of the current knowledge of the topic and identify relevant areas of seagrass research for the coming decade.

II. Seagrass Production

A. Seagrass Standing Stocks and Productivity

Since the pioneering work of Petersen (1914), we have accumulated a vast amount of knowledge on seagrass productivity. The 1973 International Seagrass Workshop held in Leiden resulted in one of the first comprehensive and integrative summaries of seagrass ecosystems (McRoy and Helfferich, 1977). Based on a synopsis of existing literature at the time, McRoy and McMillan (1977) concluded that seagrass beds were among the most productive and complex of oceanic ecosystems. Most importantly, they recognized that seagrasses themselves were often just one component of a highly diverse ecosystem that also included significant contributions of other primary producers, including benthic micro- and macroalgae, epiphytic algae, and phytoplankton.

For seagrasses, net primary production is extremely variable (see Table 1, Larkum et al., Chapter 14) and only tentative ranges and average values can be provided. The compilation of Duarte and Chiscano (1999) indicates that above-ground production ranges from 0.003 to 15 gDW m^{-2} day^{-1}. In terms of carbon, estimates range from 0.1 to 18.7 gC m^{-2} day^{-1}, but average 0.5–2.0 gC m^{-2} day^{-1} for most beds with above-ground biomass >50 gDW m^{-2} (Stevenson, 1988; Dawes, 1998). These rates roughly correspond to productivity:biomass ratios (P:B ratios) of about 1–5 for populations in subtropical and temperature latitudes (Duarte, 1989) and are equivalent to 300–1500 gC m^{-2} year^{-1} based on the wide range in seagrass standing stocks and productivity rates reported in the literature. This high annual productivity demonstrates that seagrasses stand out when compared with other aquatic and terrestrial producers (Table 1).

An important realization over the last decade was that previous seagrass production assessments using leaf marking techniques (e.g. Zieman, 1974; Vermaat et al., 1987) probably underestimated total production. Below-ground to above-ground ratios of seagrass biomass are often >1, ranging from 2 to 5 for many systems and species (McRoy, 1974; Kirkman and Reid, 1979; West and Larkum, 1979; Zieman, 1982; Sand-Jensen and Borum, 1983; Kenworthy and Thayer, 1984; Brouns, 1985; Dunton,

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Abbreviations: δ^{13}C – ratio of ^{13}C to ^{12}C based on a belemnite standard; δ^{15}N – ratio of ^{15}N to ^{14}N; δ^{34}S – ratio of ^{34}S to ^{32}S; DIC – dissolved inorganic carbon; DOC – dissolved organic carbon; DP – detrital production; GC – grams carbon; GDW – grams dry weight; NPP – net primary production; PAM – pulse amplitude modulated (fluorometer); PLFA – polar lipid-derived fatty acid; P:R ratio – photosynthetic rate to respiration rate ratio; RA – refractory accumulation; RPD – redox potential discontinuity.

1996). Thus, below-ground production ranges from 0.001 to 20 gDW m^{-2} day^{-1} (Duarte et al., 1998; Duarte and Chiscano, 1999; Kaldy and Dunton, 2000). Only recently, however, have the importance of below-ground tissues for carbon storage and in-sediment biogeochemical processes been recognized in plant production models.

B. Contribution of Epiphytes and Other Primary Producers

In addition to understanding the factors that control carbon flow through food webs, it is necessary to determine the trophic importance of components of the seagrass food web, which are often overlooked. On a broad level, the extent to which these food webs depend on locally-derived food resources vs. more transient planktonic resources needs to be quantified. Although locally-generated production is high in seagrass systems, organic matter flux through the planktonic and filter-feeding pathways may be significant as well. At a finer level, and as will become evident below, the relative contribution of the resident producers must be better understood: algal epiphytes and other primary producers (e.g. drift macroalgae, benthic macroalgae, and phytoplankton) have long been recognized as significant contributors to total seagrass bed primary production (McRoy and McMillan, 1977), yet their quantitative role has been neglected (Fry et al., 1987). Because sediments within and between seagrass beds constitute a large area in the seagrass landscape, it is likely that the role of sediment microalgae may have been largely underestimated. Algal epiphyte contribution alone has been reported to range from 20 to 60% (see review by Borowitzka and Lethbridge, 1989; see also Borowitzka et al., Chapter 19). More recently, Moncreiff et al. (1992) reported algal production (including epiphytes, benthic diatoms, and phytoplankton) to be 87% of total system production in Mississippi Sound. As described in detail later, Moncreiff and Sullivan (2001), Dauby (1989), and Yamamuro (1999) have recorded the large contributions of algae in seagrass beds, and stand in contrast to many studies which concentrate only on the importance of seagrass carbon both within and outside seagrass communities (see review by Stevenson, 1988 and Section 3.4.1).

Kaldy et al. (2002), for example, showed that benthic macroalgae accounted for most of system net primary production (33–42%), followed by seagrasses (33–38%) and other microalgae (23–56%). Furthermore, this is a role that may be increasing in coastal and estuarine systems that are becoming increasingly more eutrophic due to nitrogen loadings from adjacent watersheds (Hauxwell et al., 2003). By incorporating the sediment microalgae into future studies, a more complete picture of trophic dynamics can be developed that will allow us to generate a landscape perspective (see Bell et al., Chapter 26) of the flux of carbon and nutrients, related to variables such as depth, irradiance, nutrient availability, and sediment type.

C. Seagrass Production Measurements

For decades, seagrass productivity estimates have been based on the hole-punching (Zieman, 1974). Alternatively, for plants with very narrow blades, cut and harvest approaches have been employed (Virnstein, 1982). Neither method accounts for below-ground production, which as mentioned earlier, can be greater than 50% of total seagrass production. Other problems include tissue loss by grazing or mechanical damage and physiological disturbance associated with clipping (Tomasko and Dunton, 1995; Kowalski et al., 2001).

More sophisticated approaches to net production measurements have included *in situ* measurement of whole plant photosynthetic oxygen evolution and respiration using chambers in combination with continuous measurements of underwater irradiance at canopy level (Herzka and Dunton, 1997, 1998). This approach is not only extremely labor intensive but requires comprehensive knowledge of seagrass photosynthetic response to temperature and light. Alternatively, various researchers have employed a whole plant approach based on laboratory determinations of plant photosynthetic parameters (Zimmerman et al., 1989; Fourqurean and Zieman, 1991). In either case, the method is labor intensive and requires continuous in situ measurement of underwater irradiance to calculate daily or annual net production. These physiological measurements normally measure oxygen evolution or carbon uptake, and the inherent errors related to internal recycling or storage of gases, contributions by other organisms (such as bacteria, epiphytes, and macroalgae), and the photosynthetic quotient make either approach problematic (see Mateo et al., 2001).

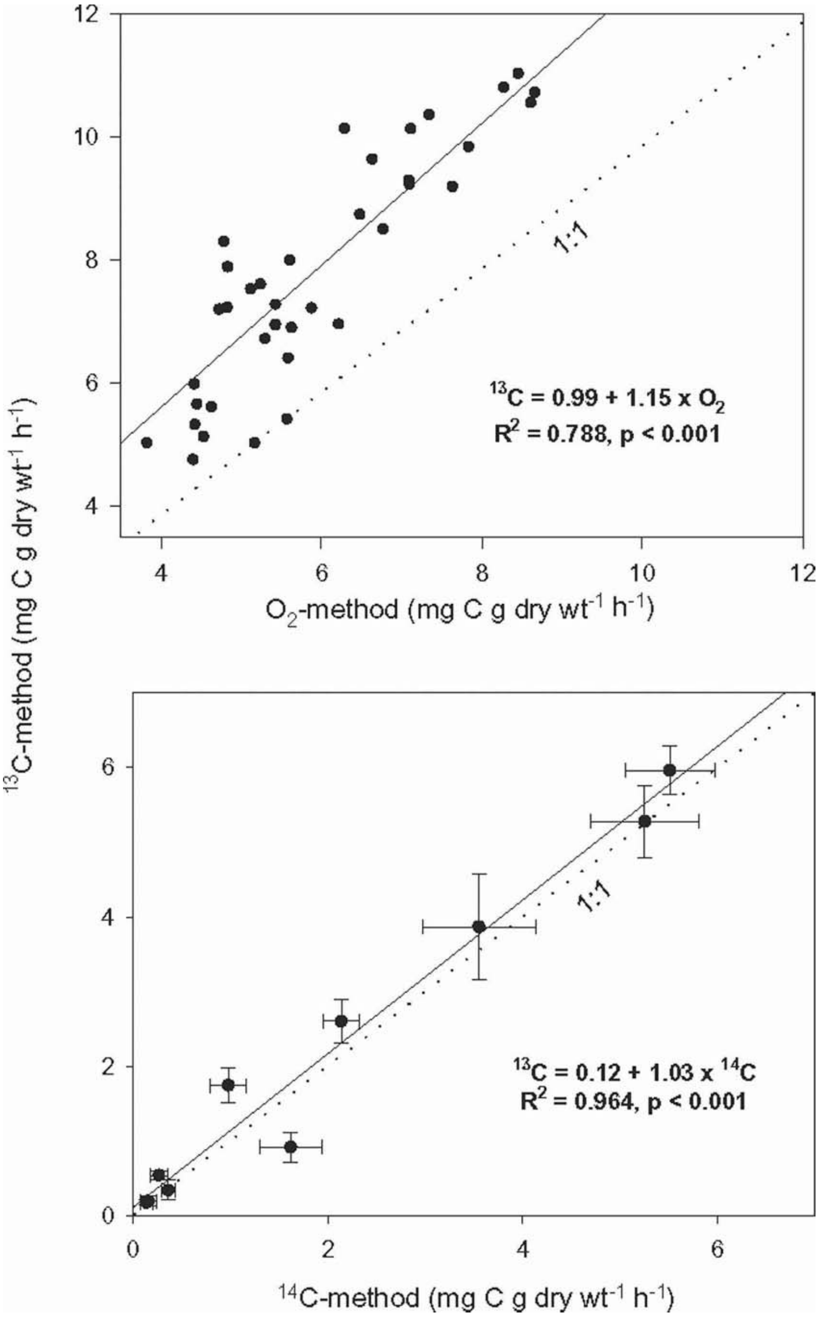

Fig. 1. Comparison of the ^{13}C, ^{14}C, and O_2 methods for estimating carbon uptake rates in *Zostera marina* (modified from Mateo et al., 2002).

Recent advances in both mass spectrometric analyses of stable isotopes and chlorophyll fluorescence measurements have presented some promising opportunities for seagrass biologists. Direct measurement of carbon uptake by seagrasses and other large macrophytes has always proved difficult, using ^{14}C uptake methods, due to expense and hazards associated with its use and disposal. However, both Mateo et al. (2001) and Miller and Dunton (2003) have recently demonstrated the application of ^{13}C to measurement of carbon uptake rates in both seagrasses, and large macroalgae (kelp), respectively (Fig. 1). Challenges with the ^{13}C method include access to an isotope ratio mass spectrometer (IRMS), accurate knowledge of the $\delta^{13}C$ ratio of the dissolved inorganic carbon (DIC) pool, and the labor associated with sample preparation. Despite these limitations, isotopic labels of ^{13}C and ^{15}N can provide substantial insights to critical processes affecting seagrass productivity including carbon and nitrogen cycling and storage, epiphytic effects on seagrass photosynthesis, and carbon translocation within various tissue compartments.

Pulse-amplitude modulated (PAM) fluorescence has been used to examine seagrass photosynthetic characteristics (Ralph et al., 1998; Beer and Bjork, 2000; Durako and Kunzelman, 2002; Larkum et al., Chapter 14). Currently, PAM fluorescence not only measures leaf photosynthetic potential (Fv/Fm), but provides a non-invasive opportunity to assess photosynthetic electron transport (approx. equivalent to gross photosynthesis). Although PAM fluorescence facilitates photosynthetic response determinations, the method does not allow linkage between photosynthetic electron transport rates and net productivity, because respiratory rates are not measured. Consequently, PAM fluorescence has been limited in its application to primary productivity measurements, and awaits further development of reliable P/R ratios.

D. Light and Carbon Metabolism in Seagrasses: Whole Plant Models

Seagrass distribution and productivity are largely regulated by variations in light attenuation through the water column (Fig. 2). This is especially true in coastal regions, where declines in water quality from human encroachment have caused worldwide losses of seagrasses (Dennison et al., 1993; Walker et al., Chapter 23). Decreased water transparency from river discharge, devegetation (causing higher resuspension of sediments), dredging activities, excess phosphorus and nitrogen loading, which promotes pelagic, epiphytic, and benthic algal blooms, etc., reduces light availability for photosynthesis, ultimately causing significant loss of productivity and biomass as plants retreat from deeper waters (Onuf, 1994; Hauxwell et al., 2003; see Walker et al., Chapter 23).

Negative effects of nutrient enrichment on submerged aquatic vegetation in eutrophic systems through algal overgrowth have been widely observed (Duarte, 1995). However, a recent study by Heck et al. (2000) contradicted this accepted notion. Based on well-designed field experiments that combined the effects of top predators and nutrient additions in a *Thalassia testudinum* community, Heck et al. (2000) found that nutrient enrichment had no significant effect on epiphyte biomass or *T. testudinum* productivity (see also Heck and Orth, Chapter 22). Instead, Heck et al. (2000) determined that the manipulation of top predators in the system resulted in the most significant effects on epiphyte biomass and seagrass productivity, complicating the simple paradigm between nutrient enrichment, light alteration, and seagrass productivity proposed by Duarte (1995). This example suggests that the paradigm of eutrophication always having negative effects needs to be closely scrutinized (see also Marbà et al., Chapter 6).

The critical role of below-ground tissues as carbohydrate storage organs, sinks for photosynthetically evolved oxygen and osmoregulation sites was summarized by Touchette and Burkholder (2000). The below-ground tissues of seagrasses are often a major component of the total biomass and serve as a photosynthetic reservoir that supports growth and maintenance of other tissues during periods of low photosynthetic production (Pirc, 1989; Burke et al., 1996; Alcoverro et al., 2001) and also CO_2 generated in the roots and rhizomes may be a significant source of carbon for the leaves (Borum et al., Chapter 10).

Reliable seagrass biomass and productivity models have been generated based on both above- and below-ground tissues and mass carbon balance calculations (Wetzel and Neckles, 1986; Alcoverro et al., 2001; Burd and Dunton, 2001). Zimmerman (2003) (see also Zimmerman, Chapter 13) took another approach and developed a sophisticated model that predicts seagrass canopy photosynthetic performance in response to a variety of variables, including canopy architecture, leaf orientation, and water quality (although the model so far does not incorporate epiphytes). It is apparent that the development of predictive seagrass productivity models requires further research on carbon partitioning among seagrass compartments, especially under light-limited conditions, and long-term in situ measurements of seagrass productivity under recorded light and water quality conditions.

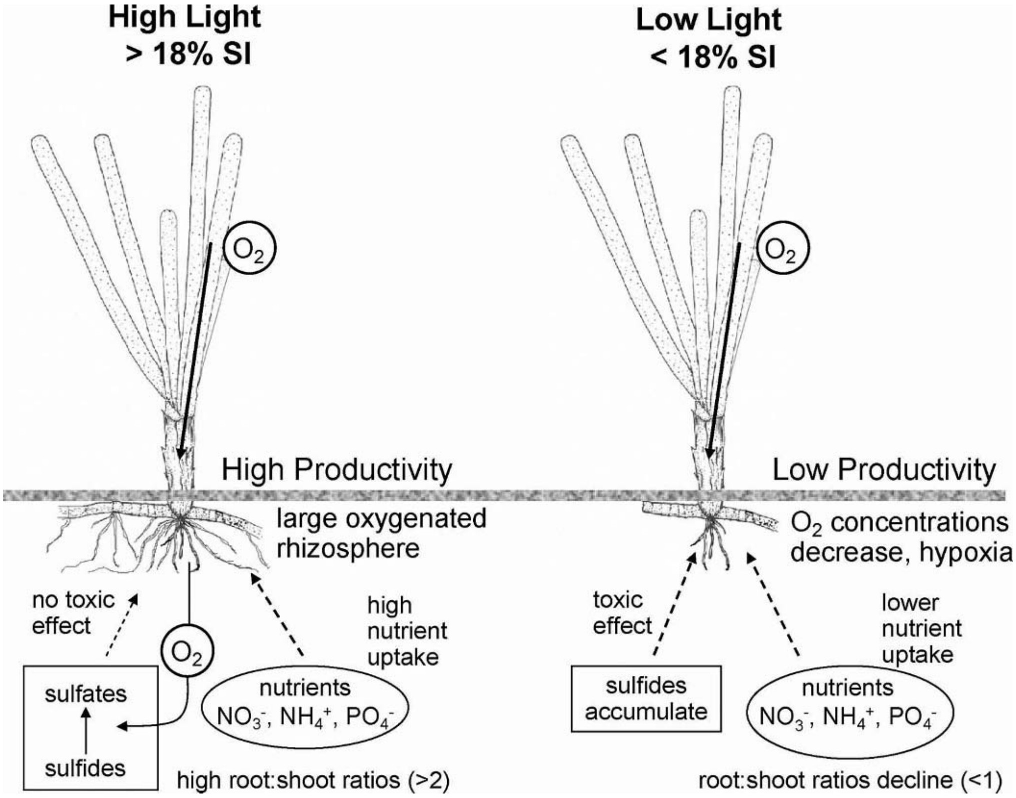

Fig. 2. Effect of light attenuation on seagrass productivity, sediment chemistry, and root:shoot biomass ratios. Photosynthetic oxygen transported into seagrass roots and rhizomes plays a significant role in the maintenance of aerobic conditions in the rhizosphere. Light attenuation that drops the percent surface irradiance (SI) to less than 18% (for seagrasses in the northwestern Gulf of Mexico) produces less oxygen for below-ground tissue respiration, which can result in build-up of sulfides and ammonium, toxic to seagrasses at high concentrations.

III. The Fate of Seagrass Production

As an essential part of the ecological approach to material cycles in the biosphere, the study of the fate of organic matter is of equal importance to the study of primary production itself. For instance, the amount of seagrass production that is consumed by herbivores and decomposers sets limits to the level of secondary production that can be maintained by the bed (Cebrián and Duarte, 1998). Similarly, the capacity of seagrass beds to act as sinks of organic matter depends on how much production is left over by herbivores and decomposers and subsequently accumulated as refractory matter in the bed (Duarte and Cebrián, 1996; Mateo and Romero, 1997).

The fates that seagrass production may endure are related by the following mass-balance equations:

$$\Delta B_t = \mathrm{NPP} - \mathrm{H} - \mathrm{DP} \quad (1)$$

$$\Delta \mathrm{DM}_t = \mathrm{DP} + \mathrm{I} - \mathrm{D} - \mathrm{E} - \mathrm{RA} \quad (2)$$

where ΔB_t (the living compartment) and $\Delta \mathrm{DM}_t$ (the detrital compartment) are the changes in seagrass biomass and degradable detrital mass per unit time, respectively, and the other terms are NPP—the temporal rates of net primary production, H—herbivory, DP—detrital production, I—import, D—decomposition, E—export, and RA—refractory accumulation. Units for all these fates are usually reported in gDW per square meter per unit time. Equation (1) corresponds to the living compartment, and it states that any temporal change in seagrass biomass corresponds to the difference between production and the loss processes of herbivory and detrital production. Detrital production, in turn, includes wasteful removal by herbivores, exudation of dissolved organic matter, natural mortality through senescence and infectious mortality. Equation (2) corresponds to the detrital compartment, and states that any temporal change in degradable detrital mass is the difference between the gain processes of detrital production and import and the loss processes of decomposition, export, and refractory accumulation. The following sections contain a selective discussion of the variability, controls, and consequences of the routes listed in Eqs. (1) and (2). The two main objectives of this discussion are to (i) summarize some important patterns in our current knowledge and (ii) identify gaps that merit further research.

A. Herbivory

1. The Extent of Herbivory in Seagrass Beds

Herbivory may vary widely both within and among seagrass species. Some species, such as the mediterranean Neptune grass (*Posidonia oceanica*), tend to have modest levels of herbivory (i.e. <10% of aboveground production consumed by herbivores; Pergent et al., 1994; Cebrián et al., 1996a), although occasionally this species has been shown to support substantial herbivory (Kirkman and Young, 1981; Shepherd, 1987). Other species, such as turtle grass (*T. testudinum*), often support larger levels of consumption, although this may have been more important in pre-columban (ca. 1500 AD) times when abundances of turtles, manatees, dugongs, and other large grazers were high, before the current centuries of heavy human exploitation. Indeed, intense grazing on turtle grass does not seem uncommon (Valentine and Heck, 1991; Heck and Valentine, 1995; Valentine et al., 2000; Valentine and Duffy, Chapter 20). However, even for species that often show large losses to herbivores, the spatial and temporal variability in herbivory within the species can be substantial. For instance, Cebrián and Duarte (1998) compared four turtle grass populations in the Caribbean and found that the percentage of primary production consumed by herbivores ranged between <1 and 30% among the populations. Many other examples of large within-species variability in herbivory exist (Cebrián et al., 1996b; Valentine and Heck, 1999; Valentine et al., 2000).

So what generalities can be made about the magnitude of herbivory for seagrasses? Figure 3A and B includes an extensive compilation of published values of herbivory made for this chapter (data set and further explanations are available at 'http://ecosystemslab.disl.org' under 'data sets'). It can be seen that the percentage of above-ground production removed by herbivores is skewed to the right, with most populations losing <10% of the above-ground production to herbivores. While herbivory is an inherently variable process, the number of studies reporting modest levels of herbivory largely exceeds those reporting intense herbivory (but see Valentine and Duffy, Chapter 20).

An important difference emerges depending on whether herbivory is regarded as absolute consumption or as the percentage of seagrass production consumed. While the percentage formulation tends to be modest, because of the high levels of above-ground production that seagrasses often reach, the values of absolute consumption tend to be higher and similar to those observed for many other aquatic and terrestrial producers (Cebrián and Duarte, 1994; Cebrián et al., 1998; Cebrián, 1999, 2002).

Thus, in general, seagrasses transfer a significant quantity of biomass to herbivores despite appearing to have only a modest percentage of production removed. This dichotomy suggests two important corollaries. First, it appears that herbivores generally have a limited role in constraining seagrass biomass since they often remove <10% of the plant production. Second, and despite the seemingly modest role of herbivores, seagrasses seem to have the capacity to fuel significant levels of herbivore production in comparison to the levels supported by other aquatic and terrestrial producers. The large variability in herbivory found within and among seagrass species indicates that numerous mechanisms can influence this process. One such mechanism is herbivore abundance. The influence of herbivory abundance has been particularly well demonstrated for sea urchins. Sea urchin densities are often strongly regulated by the intensity of predation on young recruits (Sala, 1997; Sala et al., 1998). Under relaxed predation, sea urchins may become abundant and inflict substantial damage in nearby seagrass beds (Keller, 1983; Larkum and West, 1990; Klumpp et al., 1993; Greenway, 1995; Rose et al., 1999). The increase in sea urchin density may be enormous, leading to population outbreaks and the subsequent decimation of large seagrass areas (Camp et al., 1973; Larkum and West, 1990; Macia and Lirman, 1999; Rose et al., 1999).

Another well-known source of variability is the 'cultivation' feeding pattern that some vertebrate herbivores, such as green turtles (Bjorndal, 1980; Zieman et al., 1984) and dugongs (De Iongh et al., 1995; Preen, 1995) exhibit. These herbivores feed

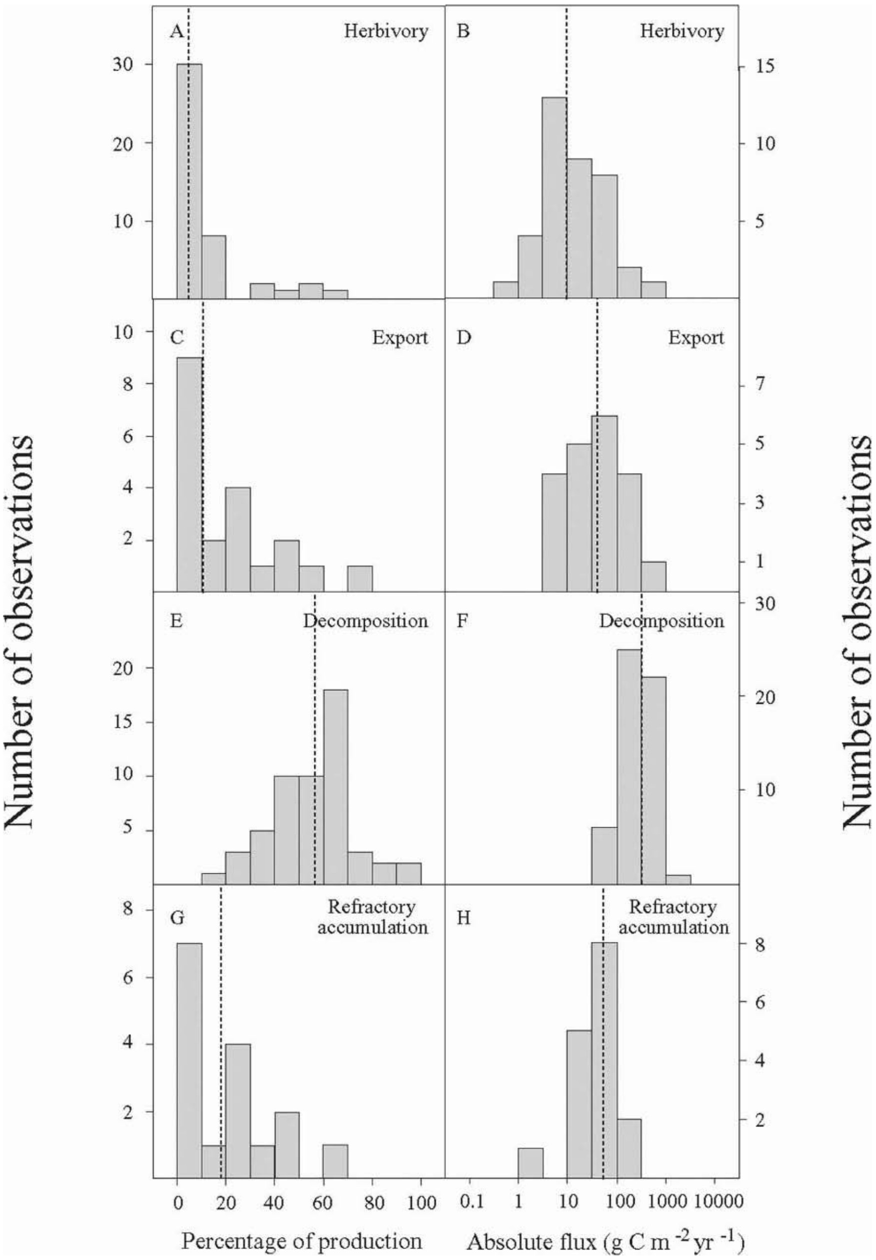

Fig. 3. The histograms of (A) the percentage of seagrass leaf production consumed by herbivores, (B) absolute consumption, (C) the percentage of leaf production exported, (D) absolute leaf litter export, (E) the percentage of total (sum of below- and aboveground) seagrass production decomposed, (F) absolute decomposition, (G) the percentage of total seagrass production accumulated as refractory detritus, and (H) absolute seagrass refractory accumulation. Dashed lines represent the medians.

recurrently on the same seagrass plots for a sustained period of time, thereby keeping the blades tender and young and maximizing the intake of nutrients and energy. After a variable period of time, the herbivores abandon those plots and start ‘cultivating’ new ones.

2. The Role of Nutrients in Herbivory

One regulating factor that has received considerable attention is the nutrient content of seagrass leaves with the suggestion by several authors that the extent of herbivory is limited by the nutrient

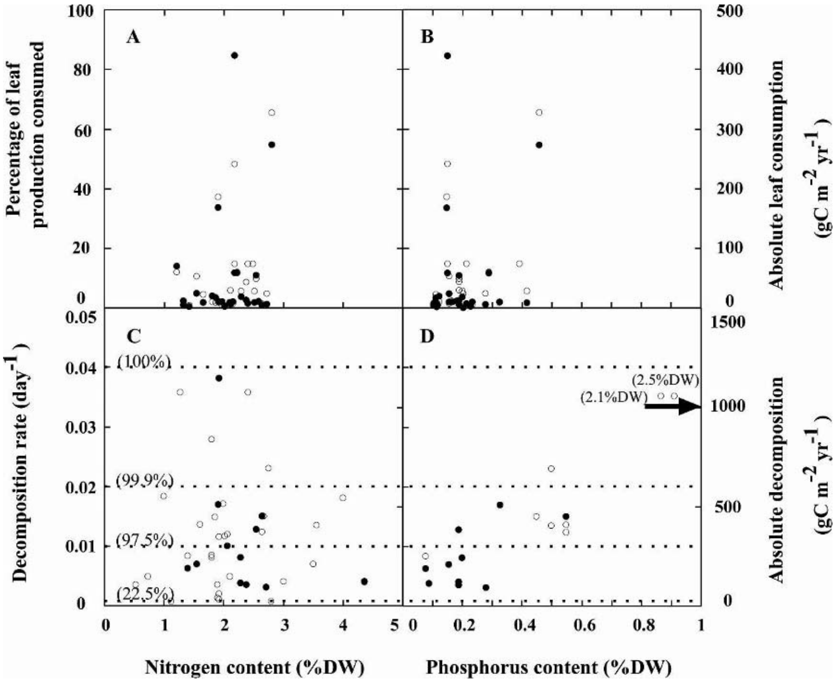

Fig. 4. The relationships between (A) the percentage of leaf production consumed by herbivores and absolute consumption, and leaf nitrogen content; (B) the percentage of leaf production consumed by herbivores and absolute consumption, and leaf phosphorus content; (C) decomposition rates and absolute decomposition, and detritus nitrogen content; (D) decomposition rates and absolute decomposition, and detritus phosphorus content. Open circles correspond to the percentage of leaf production consumed or decomposition rates, and closed circles to absolute consumption or absolute decomposition. The dashed lines in (C) and (D) correspond to the percentage of detritus production decomposed within 1 year for that given decomposition rate, which has been calculated as $(1 - e^{-k \cdot 365}) \times 100$ and where k is the given decomposition rate (Olson, 1963). Values in (A) and (B) correspond to leaves, and in (C) and (D) most values correspond to leaves and a few of them to below-ground (rhizomes and roots) organs. The relationships between decomposition rates and nitrogen and phosphorus content are mostly redrawn (i.e. we just include a few more values) from Enríquez et al. (1993), whereas the rest of relationships are original to this contribution. The two points right above the arrow in (D) correspond to the highly questionable values of detritus phosphorus content (in parenthesis) reported by Pellikaan (1984) (see text). Those values are off the scale used in the panel, as is indicated by the arrow.

content of the leaves, with higher nutrient content being conducive to greater herbivory (Bjorndal, 1980; Lalli and Parsons, 1993; Duarte, 1995; Valiela, 1995). This contention is primarily based on observations that grazing rates by selective vertebrate herbivores, such as parrotfish, green turtles, and dugongs, are positively correlated to higher nutrient contents (Zieman et al., 1984; Williams, 1988; McGlathery, 1995; Preen, 1995). However, as recent research has shown, greater herbivory pressure is not always associated with higher nutrient contents (see also Valentine and Duffy, Chapter 20). For instance, Cebrián and Duarte (1998) compared several populations of nine seagrass species encompassing a broad latitudinal range and found no significant relationship between herbivory and leaf nitrogen and phosphorus content across species and, with the exception of *Cymodocea nodosa*, across the populations of any given species, possibly because a substantial fraction of the nutrients may be bound to fibrous compounds (i.e. lignin) and thus indigestible to many herbivores (Thayer et al., 1984; Choat and Clements, 1998). In addition, Valentine and Heck (2001) have shown that the intensity of grazing by the pink sea urchin (*Lytechinus variegatus*) on turtle grass does not increase with leaf nutrient content.

Figure 4 gives values of leaf nutrient content for a subset of the herbivory values. There appears to be very little correlation between leaf nitrogen and phosphorus contents and herbivory, either expressed in absolute terms or as the percentage of production consumed. The correlation coefficients between the percentage consumed and leaf nutrient content ($R = 0.29$, $p = 0.14$ for nitrogen content and $R = 0.37$, $p = 0.05$ for phosphorus content; Fig. 4A and B, respectively) are possibly suggestive, but they do not allow for any robust conclusion. Clearly, more work is needed to understand the existing controversial observations of the association between seagrass leaf nutrient content and the intensity of herbivory. Given the high spatial and temporal variability that herbivory may show in nature (see above), it seems possible that the different spatial and temporal scales covered by these studies confounds any firm conclusion.

An important point to be made is that, of the carbon consumed by herbivores, only a very small fraction will be assimilated and effectively incorporated in the secondary production compartment. For example, it has been shown that the carbon assimilation efficiency of the main grazer of Neptune grass in the Mediterranean, the fish *Sarpa salpa*, is as low as 0.2% (Velimirov, 1984). In fact, it is not uncommon to observe entire, green fragments of Neptune grass leaves (ca. 0.8 cm^2) being defecated to the bed sediments from schools of this fish (personal observation). For *P. australis* on the East coast of Australia, the value was 3% for the main grazing fish, *Monacanthus chinensis* (Conacher et al., 1979). In tropical seagrass stands, grazing by macroinvertebrates can be substantial. Gammarids of the genus *Ampithoe* in Fiji grazed half the leaf carbon production of *Syringodium isoetifolium*, but assimilated only 10% of it (Mukai and Iijima, 1995). More than half of the carbon grazed was respired and the rest excreted and defecated. Thus, most grazing rates given in the literature may be large overestimates of the actual carbon flux from producers to consumers. A detailed knowledge of assimilation rates for the various herbivores should be acquired and used to correct the fluxes accordingly.

B. Export

The export of materials from seagrass beds has many important implications for surrounding communities and ecosystems (Romero et al., Chapter 9; Kenworthy et al., Chapter 25; Bell et al., Chapter 26). Since most exported detritus is decomposed in downstream systems (Mann, 1988), the quantity of detritus exported sets the limits to the levels of secondary production that the bed can support beyond its boundaries (i.e. allochthonous secondary production; see Chapters 25 and 26). Since export represents a nutrient loss for the bed, these losses must be compensated by exogenous nutrient inputs (Duarte and Cebrián, 1996; Mateo and Romero, 1997; Romero et al., Chapter 9).

Despite the importance of export in seagrass-dominated coastal ecosystems, few reports exist on its impact on bed economy. This oversight may be due to three inherent technical difficulties.

First, and most importantly, seagrass beds are often open systems and have widespread exchange with offshore waters, driven by the interaction of several forces, including wind, tides, and waves. This renders measurement of detrital export difficult. Most measurements of detrital export are limited to specialized systems connected to open waters through narrow outlets (e.g. coastal lagoons).

Second, the boundaries of seagrass beds, which define the location at which export measurements are taken, are sometimes difficult to define with certainty, making measurements somewhat arbitrary.

Third, detrital traps used to derive direct estimates of export are difficult to deploy.

These methodological limitations have discouraged researchers from quantifying detrital export from seagrass beds and have resulted in a scarcity of publications on the issue. These problems emphasize the importance of developing alternative methods. Romero et al. (1992) proposed an indirect method: in the hypothetical absence of export, litter stocks in the bed depend on inputs from leaf fall (the main source of variation being depth) and outputs due to remineralization. Leaf fall rates can be estimated as the difference between primary production (using the method described in Zieman, 1974) and biomass increase. Decay rates can be approximated using the classical in situ litter bag incubations. This can be expressed mathematically in order to predict litter accumulation in a given moment and a given place in the bed.

$$L'_i = F_i \mathrm{e}^{(-kt/2)} + L_{i-t}\,\mathrm{e}^{(-kt)} \tag{3}$$

where L'_i is the predicted standing litter at time i, F_i is the weight of leaf fallen between times i and $i-1$, t is the time interval between consecutive samplings, k is the decay rate for this period and area (e.g. depth), and L_{i-t} is the standing litter observed in situ at time $i-t$ (i.e. before the initiation of the period). Knowing the standing litter stock at the end of the period L_i (sampled in the field), export (E_i) can be calculated as the difference

$$E_i = L'_i - L_i \tag{4}$$

Such an approach entails intensive field effort, requiring estimates of leaf input, litter decay, and litter stocks throughout the year, and it possibly underestimates discontinuous export events. Nevertheless, all the methods required are robust, easy to apply, and integrate changes over long time. Therefore, this should be a useful integrative approach for future studies.

The few reports indicate that export can vary from 0 to 100% of total production (e.g. Bach et al., 1986; Hemminga and Nieuwenhuize, 1990; Stapel et al., 1996; Mateo and Romero, 1997; Ochieng and Erftemeijer, 1999; Hemminga and Duarte, 2000). This large variability results from the high variability of the intensity of physical energy in the bed, the major driving force (Josselyn et al., 1983; Bach et al., 1986; Fry and Virnstein, 1988; Mateo et al., 2003; Mateo and Rossi, submitted; Section II.A of Koch et al., Chapter 8). Weather, tides, and the degree of bed exposure (i.e. area of open water or fetch and openness to offshore waters) dictate this intensity. The crucial role of physical energy is shown by supralittoral deposits in different ecosystems. The largest accumulations of seagrass leaf litter cast on beaches have been reported in a small Mediterranean exposed bay (Tabarca Island, Alicante, Spain) for the species *P. oceanica* (Mateo et al., 2003; Fig. 5, left and top right); the distribution and height of the deposits (‘banquettes’) accurately described the water energy reaching the perimeter of the bay, with leaf litter accumulation in amounts from 18 to 500 kg of dry wt.(m shoreline)$^{-1}$, at both ends and in the center of the bay, respectively (see also Kuo and den Hartog, Chapter 3 for *P. australis* examples). The authors estimated for the *P. oceanica* example that the total supralittoral deposits represented 50.7, 71.0, 27.2, and 8.7% of the annual bed dry weight, carbon, nitrogen, and phosphorus production, respectively. They concluded, however, that the deposits were only temporary sinks because the accumulated material can eventually return to the water (Fig. 6). At the other extreme, export figures for *C. nodosa* leaf litter in a semi-enclosed estuarine bay (Alfacs, Tarragona, Spain) were found to be almost negligible due to the rapid wave energy dissipation against the embayment shore (the relative proportions being 0.26, 0.27, 0.27, and 0.16% of the annual bed dry weight, carbon, nitrogen, and phosphorus production, respectively; Mateo and Rossi, submitted). Some seagrass species have long, bulky leaves that sink soon after shedding, whereas others produce light, thin leaves that can float for long periods before sinking and are thus, more likely to be exported. Zieman et al. (1979) provided the first example of the importance of leaf buoyancy. They compared adjacent beds of the relatively broad-leaved turtle grass (*T. testudinum*) with beds of the thin-leaved manatee grass (*Syringodium filiforme*), and showed that, whereas turtle grass exported 1% of its leaf production, manatee grass exported 75%.

Export of below-ground parts is rarer and only strong storms can carry significant amounts out of the bed or throw them onto the beach (Bach et al., 1986; Fig. 5, bottom right).

In many temperate systems, autumn is characterized by high absolute amounts of litter export because many seagrass species shed most of their leaf biomass at this time (Cebrián et al., 1997; Mateo and Romero, 1997; Hauxwell et al., 2003). Accordingly, Bach et al. (1986) surveyed leaf export from an eelgrass bed in Phillips Island (NC, USA) monthly over 1 year and found the greatest levels of absolute export in late August, which was also the period of maximum leaf shedding. However, ecologically meaningful export rates are those relative to detritus production or to plant requirements. In a seasonal study of leaf litter export in a *P. oceanica* bed, Mateo and Romero (1997) found that the highest export losses relative to detritus production occurred from February–May although maximal litter stocks were recorded during July–October.

The nutritional quality of seagrass leaf litter is often strongly correlated with decomposition rates, which in turn influence export (Mateo and Romero, 1997; Pérez et al., 2001). Thus, seagrass leaf litter nitrogen content is often positively correlated with decomposition rates although contradictory results abound (see Section III.C): if decomposition is slow there is the greater likelihood of export or burial (see Section IV.B.1). Two *P. oceanica* beds, one off Medes Islands (NW Mediterranean, Spain) and another off the Island of Ischia (Naples, Italy), both located in open areas and at similar latitudes, had a three-fold difference in export rates (higher at Ischia). The effect of waves and currents affecting both beds seemed to be different, and the different export rates were most probably associated

Fig. 5. Supra-littoral deposits of *Posidonia oceanica*. Left: Old 'banquettes' of *P. oceanica* leaf litter along the coast of Nueva Tabarca Island (Alicante, Spain). The banquettes shown are ca. 1.5 m high (photograph by J. L. Sánchez-Lizaso). Top right: Recently formed banquettes 0.5 m high from Corsica, France (photograph by M. Manzanera). Bottom right: Beach-cast detritus from *P. oceanica* below-ground organs. Rhizomes and a sheath-derived aegagropile can be distinguished (photograph by M. Manzanera).

with the different nutrient content of the leaf litter (Table 2). Nitrogen and phosphorus contents of the coarse leaf litter in Ischia were on average 0.42 and 0.039%, respectively. Equivalent figures for Medes were 1.24 and 0.067%, respectively, which are 3.0 and 1.7 times higher than those at Ischia, suggesting that leaf litter 'palatability' may be an important factor governing export rates in seagrass beds.

In comparing nutrient-rich and nutrient-poor *C. nodosa* stands growing in a semi-enclosed bay (Alfacs, Ebro River estuary, Spain), Pérez et al. (2001) obtained differences in export rates that largely support the previous contention (Table 2). Around 53% of the total annual production of plant biomass was exported in poor stands, while in rich stands this value was 3.4 times lower (15.5%). Nutrient losses were much higher in nutrient-poor stands when compared to plant nutrient requirements (Table 2).

The large variability found in the percentage of leaf production exported suggests that seagrass beds may also vary widely in their levels of dependence on imported nutrients, from negligible (i.e. beds that export <10% of leaf production) to high (i.e. beds that export >80% of leaf production) levels. On the other hand, when export is regarded as an absolute flux (Fig. 3D), another important corollary arises: in spite of substantial variability, most values of absolute export tend to be large when compared with the amount of seagrass biomass that is consumed by herbivores (Fig. 3B).

C. Decomposition

Decomposition in situ seems to be the most probable fate for seagrass leaf detritus (Fig. 3E and F) and even more so for below-ground production. Seagrass rhizomes and roots are consumed by few herbivores (Valentine and Heck, 1999) due to the compactness of the tangled web that these organs form and because they are usually buried (particularly in large bodied species) (but see Valentine and Duffy, Chapter 20) for another viewpoint on the recent geological past and evolutionary consdierarions). As a consequence, in the absence of sirenians, etc, most

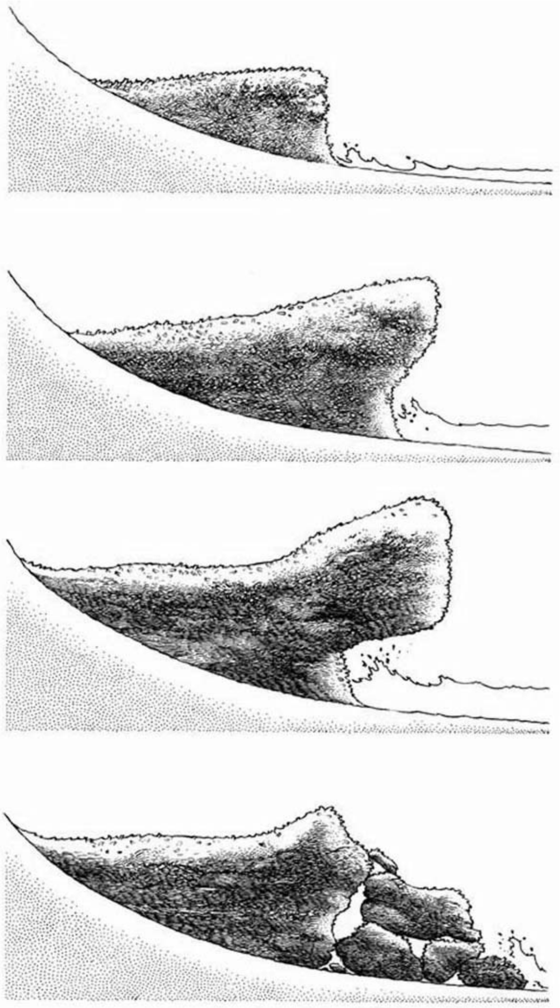

Fig. 6. Formation and destruction of *Posidonia oceanica* 'banquettes' in the Mediterranean Sea. Leaf litter accumulates on the shore by the action of strong waves forming deposits more than 2 m high. Once the maximum height has been attained, moderate wave action erodes the base of the banquette that partially collapses, returning material to the water (from Mateo et al., 2003).

below-ground production becomes detritus and decomposes within the bed, with a usually modest fraction being accumulated as refractory material (see section IV.B).

In general, the total (the sum of above- and below-ground) seagrass production that is decomposed in situ is large. The absolute amount of seagrass detritus transferred to decomposers and detritivores tends to be much larger than for many other aquatic and terrestrial producers (Cebrián, 1999, 2002). These patterns suggest two important corollaries. First, assuming that seagrass production is in steady-state (i.e. no noticeable changes across years), these results suggest that most seagrass production is supported through internal nutrient recycling. Second, seagrass beds seem to maintain high levels of secondary production by microbial decomposers and invertebrate detritivores. Thus, the abundant faunal populations that are normally associated with seagrass beds are supported mainly through the detritus-based food chain (see Section II.D.1); notice, however, that this neglects herbivory on algal epiphytes and benthic micro- and macroalgae, rich sources of food for fish in their nursery stages (see below and Borowitzka et al., Chapter 19; Valentine and Duffy, Chapter 20; and Gillanders, Chapter 21).

Seagrass decomposition can be highly variable, accounting for 15–95% of plant production (Fig. 3E) and the absolute flux to decomposers varies from 55 to 1150 gC m^{-2} $year^{-1}$ (Fig. 3F). Harrison (1989) examined the extent of decomposition variability within and among seagrass species and discussed some factors responsible for that variability. His analyses pointed to three major factors (see next sections).

1. Environmental Physical Conditions

Water temperature, sediment oxygen content, water nutrient content, and desiccation are important in decomposition. Harrison, however, gathered conflicting results as to the explicit effect of each of those physical conditions. Water temperature, contrary to what models of microbial metabolism predicted (Melillo et al., 1984), did not always stimulate decomposition rates of seagrass detritus (Walker and McComb, 1985). Some workers found higher seagrass degradation rates under anaerobic conditions (Pellikaan, 1984; Josselyn et al., 1986), consistent with the belief that most cellulose-degrading bacteria are anaerobic (Kenworthy and Thayer, 1984; Roth and Hayasaka, 1984), but contrary results have also been found (Godshalk and Wetzel, 1978; Pellikaan, 1984). Water nutrient content is important because the activity of decomposers is frequently limited by nutrient availability (Melillo et al., 1984), but again, higher nutrient concentrations in the water column did not always enhance degradation (Harrison and Mann, 1975; Fenchel and Harrison, 1976). Available reports on the effect of desiccation on the decomposition of seagrass detritus also showed discrepancies (Harrison and Mann, 1975; Zieman, 1975; Josselyn and Mathieson, 1980).

Table 2. Leaf litter nutrient content and biomass, and export of carbon, nitrogen, and phosphorus in nutrient-rich and nutrient-poor *Posidonia oceanica* and *Cymodocea nodosa* meadows. Export % is referred to annual leaf-blade production. Nutrient content % expressed on a dry weight basis. Values for Ischia Island (Naples, Italy) calculated from Romero et al. (1992); Values for Medes calculated from Mateo and Romero (1997). Values for Alfacs Bay (Ebre River estuary, Spain), calculated using data from Pérez and Camp (1986), Pérez and Romero (1994), and Pérez et al. (2001). Values have been rounded for the sake of clarity.

Species	Location	Nutrient content (%) N	Nutrient content (%) P	Decay rate (day^{-1})	Export (%) DW	Export (%) C	Export (%) N	Export (%) P	Depth (m)
Posidonia oceanica	Ischia	0.4	0.04	0.009	60	56	30	21	1–30
	Medes	1.1	0.07	0.022	10	6	6	4	5–15
Cymodocea nodosa	Alfacs-poor	2.0	0.05	0.009	53	50	42	21	0.5–1
	Alfacs-rich	2.5	0.15	0.015	16	15	15	20	0.5–1

2. Nutrient Content of Detritus

From the foregoing, it would be expected that detritus with higher nutrient contents would decompose faster. That hypothesis had been supported for certain types of producers, such as shrubs and trees (Melillo et al., 1982) and marsh plants (Valiela et al., 1984). However, Harrison's attempt to generalize as to whether seagrass detritus with higher nutrient concentrations decomposes faster yielded contradictory results. When comparing four reports on eelgrass, he found a significant correlation between faster decomposition rates and higher nitrogen content in leaf detritus; however, when studying four reports on turtle grass the correlation was not significant. Later, Enríquez et al. (1993) compiled a larger data set including several seagrass species and tested whether higher nutrient concentrations in the detritus were associated with faster decomposition rates across the species gathered. For 24 records encompassing six seagrass species (*Thalassia hemprichii*, *T. testudinum*, *P. oceanica*, *Zostera marina*, *Z. noltii*, and *Syringodium filliforme*), no significant correlation between faster decomposition rates and higher nitrogen content was found (Fig. 4C), but for seven records encompassing three species, they found a strong correlation between faster decomposition rates and higher phosphorus content (Fig. 4D). That strong correlation, however, was entirely driven by two anomalously high values of phosphorus content reported by Pellikaan (1984; see Fig. 4D). When those two anomalous values were eliminated, the relationship between decomposition rates and detritus phosphorus content became nonsignificant (Pearson correlation coefficient = 0.68, $P = 0.09$).

More recently, Mateo and Romero (1996) reported the results of several in situ litter bag experiments on a seasonal basis using two clearly different types of material in terms of nutrient quality, senescent and detrital *P. oceanica* leaves. The first type was 1.5 and 1.2 times richer in nitrogen and phosphorus, respectively, than the latter. For all seasons, senescent leaves decomposed faster than leaf litter (15% faster on average). In this case, a multiple variance analysis confirmed a highly significant effect of nutrient content in decay rates either in field or in laboratory incubations.

3. The Methodological Approach Used

It is obvious, as already noticed by Harrison (1989), that the type of material selected for litter bag experiments (senescent, detrital, entire, fragmented, fresh, frozen, with or without epiphytes, etc.) may strongly affect the decay rates to be obtained. Also, he noted that the length of detritus incubation was one of the most important methodological differences among existing reports. Detritus decay normally follows a decreasing exponential pattern that comprises leaching, decomposition, and slow breakdown of refractory phases (Olson, 1963; Valiela, 1995). Thus, the length of the incubation period can greatly affect the pattern obtained if it is not long enough to capture the three phases. Another important methodological disparity among studies was whether the incubation was done in field or laboratory conditions and, if done in the field, the pore size of the litter bags employed (Fig. 7, top left). Mateo and Romero (1996) evaluated in detail the extent of error attributable to particle losses

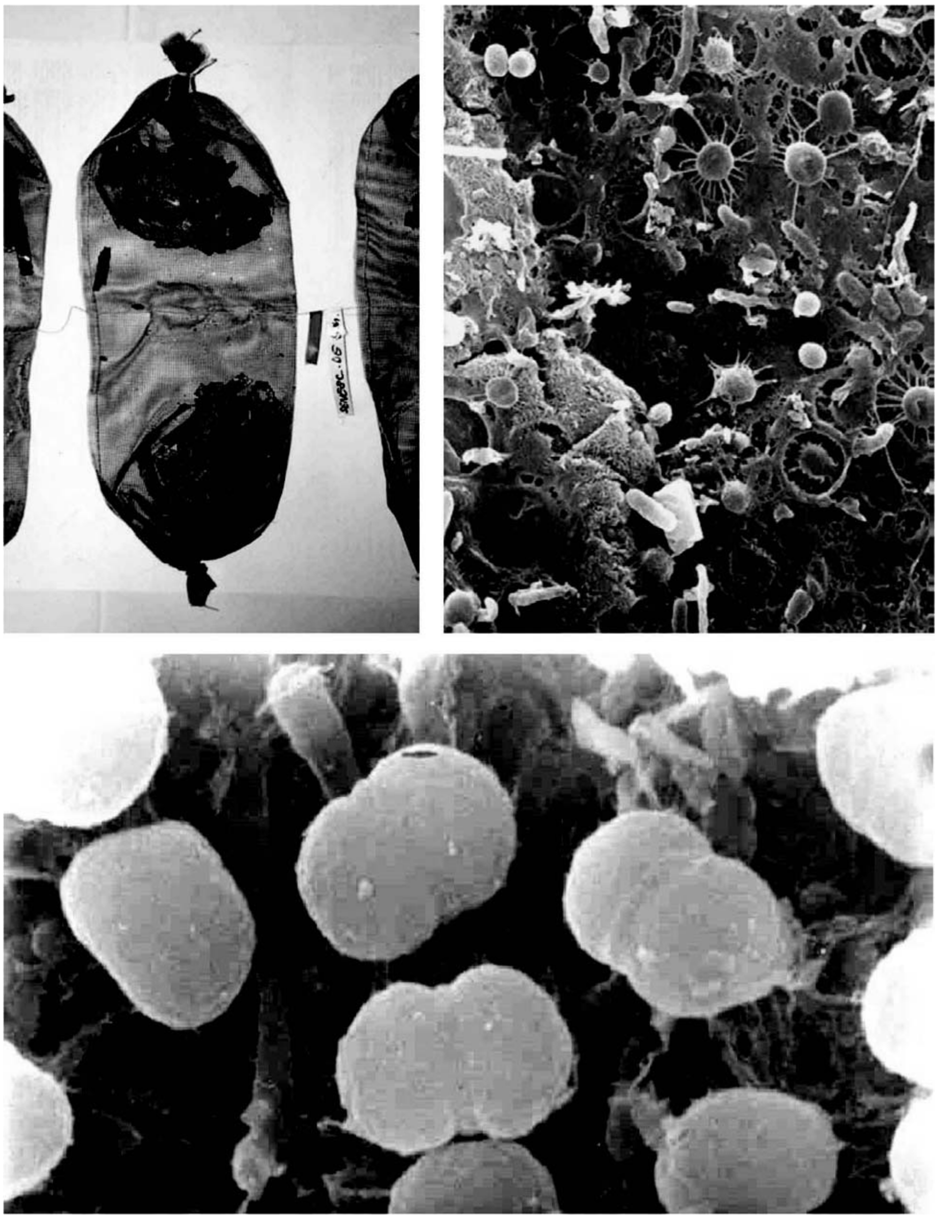

Fig. 7. Seagrass leaf litter decomposition. Top left: Typical litter bags used in the classical experiments for determining seagrass leaf litter in situ decay rates. The mesh size of the bags, as in the image, is usually 1 mm. The bags in the picture contain *Posidonia oceanica* senescent leaf litter. Top right: Round-shaped bacteria growing on *P. oceanica* leaf litter adhering by extracellular polymers. Bottom: Bacteria dividing on *P. oceanica* leaf litter (photographs by M. A. Mateo).

through the bag pores in *P. oceanica*. When comparing the results from both methods on a carbon basis, it was found that only 40% of the weight lost from the bags was actually attributable to microdecomposer activity (Figs. 7 right and bottom and 8) and the rest would seem to have been lost through the bag pores. This conclusion, however, has to be taken with caution because of the well-known limitations of microcosm experiments. However, it is also possible that respiration rates in situ may have been much higher owing to a higher water nutrient renewal.

Despite the fact that decay rate estimates using litter bags are not the most adequate for ecosystem

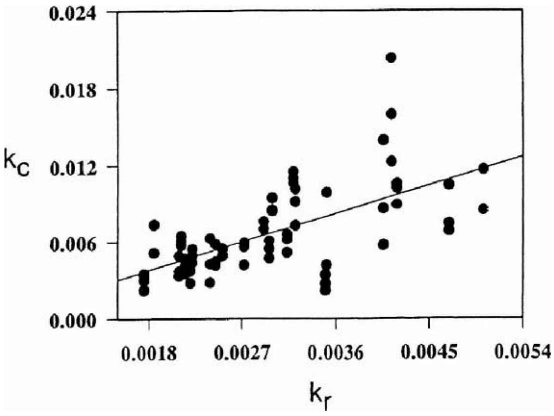

Fig. 8. Relationship between rates of carbon loss during *Posidonia oceanica* leaf litter decomposition using in situ litter bags (k_c) and litter respiration (k_r) methods ($k_c = 2.46 \cdot k_r - 0.0006$; $r = 0.63$; from Mateo and Romero, 1996).

budget studies, they have been kept for comparative purposes because of their methodological simplicity and the valuable amount of historical and recent data available in the literature derived from this approach (Short and Coles, 2001).

The work showing the prevalence of decomposition over herbivory in seagrass beds, has been the basis since the 1960s for the view that high secondary production fueled a detrital pathway using seagrass-derived carbon. Later tests, particularly using stable isotopic tracers in food web studies, have revealed that this old assumption appears to be unfounded in a growing number of cases as discussed in the following section.

D. Seagrass Food Web Studies: The Stable Isotope Approach

1. Algal vs. Seagrass Carbon Source

Stable isotope analyses have proved increasingly valuable for the study of trophic interactions within seagrass ecosystems over the past 30 years. The premise underlying their use is that the isotopic composition of an organism will reflect the composition of its food source(s) (after accounting for fractionation). Based on this simple relationship, stable isotope studies have been conducted to identify primary trophic pathways within seagrass systems from the δ^{13}C, δ^{15}N, and δ^{34}S signatures of the resident organisms. Fry et al. (1987) reviewed stable isotopic investigations in seagrass systems and recognized that ambiguities of the δ^{13}C method could often be resolved by also using nitrogen and sulfur isotopic values. In particular, it was noted that benthic (i.e. epiphytic and sediment-associated) microalgae can have carbon isotopic values similar to those of seagrass, making it difficult to assess the relative contribution of these primary producers to carbon flow through the food web. At the same time, the relative contribution of algal and seagrass organic matter to food webs differs among seagrass systems. While seagrass detritus is the dominant source of carbon in some systems, benthic and microalgal carbon dominates others.

Since Fry et al. (1987), researchers have attempted to address some of the problems inherent in stable isotope studies. Recently, Connolly et al. (2004) highlighted the effectiveness of sulfur isotopes to distinguish primary producers with similar δ^{13}C and δ^{15}N values. As such, it appears that concurrent analysis of carbon, nitrogen, and sulfur may maximize the utility of the stable isotope approach. Indeed, Moncreiff and Sullivan (2001) used stable carbon, nitrogen, and sulfur isotopic composition to trace the flow of organic matter through *Halodule wrightii* beds of Mississippi Sound, USA, and showed that benthic microalgae were the primary food source in these seagrass beds. These and other stable isotope studies conducted over the past decade have resulted in a paradigm shift in our view of seagrass trophic dynamics, from one where seagrasses were thought to be the most important material for secondary production to one in which the benthic microalgae are the major source of organic matter to higher trophic levels in seagrass food webs (Kenworthy et al., 1987; Dauby, 1989, 1995; Loneragan et al., 1997; Yamamuro, 1999; Lepoint et al., 2000).

One important advance in this direction was that achieved by Boschker et al. (1999, 2000). In an attempt to study carbon sources for bacteria they labeled, branched polar lipid-derived fatty acids (PLFAs) of bacteria to study the role of *Z. marina* carbon in several European beds. If bacterial PLFA carbon were obtained from seagrass detrital carbon, carbon isotopic ratios (δ^{13}C) of both materials should be similar. Instead, δ^{13}C values of bacterial PLFA fell between those of *Z. marina* (leaves or roots) and sediment organic matter (Fig. 9), suggesting that bacteria used a combination of both sources of carbon. However, the authors also observed that bacteria from nearby barren areas and from laboratory

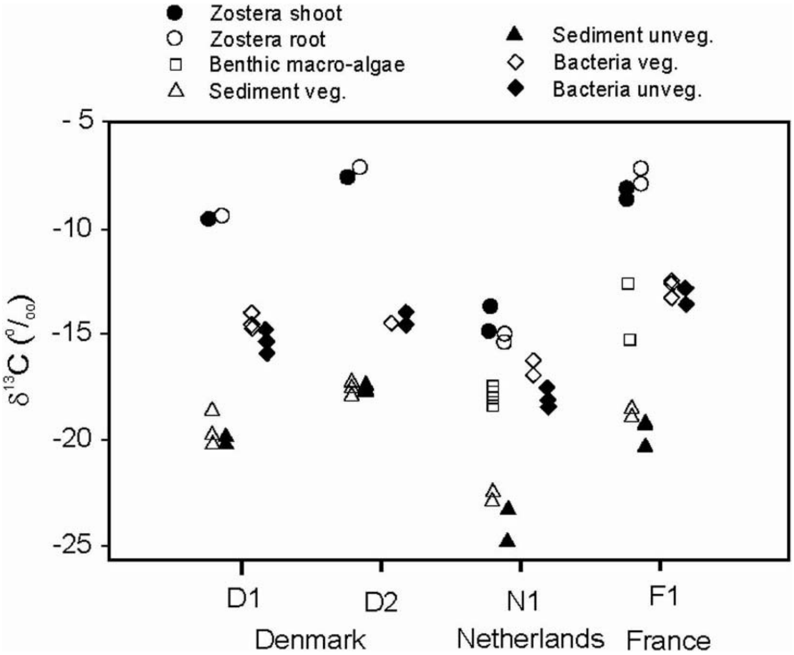

Fig. 9. Stable isotopes approach to assess the possible sources of bacterial carbon in *Zostera marina* and unvegetated sediments. Stable carbon isotope ratios in bacteria were determined in specific bacterial polar lipid-derived fatty acids (PLFAs) using specific-compound isotopic ratio mass spectrometry. D1, D2, N1, and F1 correspond to different study sites in Denmark, The Netherlands, and France, respectively (redrawn from Boschker et al., 2000).

sediment incubations had similar $\delta^{13}C$ values to those in vegetated areas. This paradox was resolved by comparing isotope ratios of benthic microalgae and bacterial biomarkers: the two being highly correlated, with the conclusion that autochthonous benthic microalgal production accounts for the abundant secondary production in these *Z. marina* beds.

Such a conclusion seems consistent with the scenarios shown in Section II.A, where seagrasses were not the dominant producers in the system (as also seen in Section II.B). Other studies have also provided evidence that seagrass contribution of organic carbon to bed sediments is only around 25–30% of the total (Simenstad and Wissmar, 1985; Dauby, 1989; Hemminga et al., 1994; Fourqurean et al., 1997; Gacia et al., 2002).

Although the relative contribution of carbon by seagrasses is lower than initially assumed, intuitively it seems that it should be substantial enough to be reflected in bacterial carbon. In another study of stable isotope ratios in PLFAs of sedimentary bacteria, Jones et al. (2003) found that the majority of sedimentary organic carbon originated from *T. testudinum* shoots and that there is tight coupling of the sedimentary bacteria and seagrass-derived organic matter. The contrasting results of Jones et al. (2003) and Boschker et al. (2000) leads one to think that there may be strong variability owing to various environmental and biological factors, as follows:

i. *Seasonality.* First, it has to be born in mind that the measurements made by Boschker et al. (2000), correspond to single sampling events. As discussed earlier, seagrass production and, therefore, detritus inputs to the sediments is seasonal and in temperate seas, with maximum production rates in summer and minimum rates in late autumn and winter (e.g. Alcoverro et al., 1998, 2001). Accordingly, leaf litter stocks in the sediment are maximum in autumn (right after leaf abscission) and minimum in early summer (Mateo and Romero 1997; see more details in Section IV.A). Thus, in autumn large inputs of fresh seagrass leaf litter may constitute the main carbon source for bacterial activity.
ii. *Export.* In Section III.B, export has been discussed in detail. Depending on seasonality, basin morphology, bed depth, hydrodynamic forces, leaf buoyancy capacity, and leaf nutrient content export can be negligible or account for the

transport of virtually the entire seagrass production out of the bed.

iii. *Low palatability of seagrass carbon.* Lower mineralization rates are shown by microbes on seagrass detritus than on macro- and microalgal detritus and this might explain why it has being observed that seagrass carbon is not the dominant carbon source for bacterial metabolism. On the other hand, Del Giorgio and Cole (1998) found that bacterial growth efficiencies were similar for macrophyte and microalgal material.

iv. *Redox conditions in sediments.* Oxygen transport from seagrass leaves to the rhizosphere oxidizes the upper few centimeters of the seagrass sediments (Figs. 2 and 10; see also Marbà et al., Chapter 6 and Borum et al., Chapter 10). Unless actively bioturbated, sediments receiving significant loads of organic matter tend to be highly reducing from the uppermost layer. Oxidizing conditions can promote rapid and dominant aerobic decomposition of fresh labile carbon (oxygen sensitive material, Hulthe et al., 1998; Kristensen, 2000). The consequence of this can be that highly palatable algal detritus is always attacked preferentially by bacteria, while seagrass detritus persists for a longer time, making it more susceptible to export or burial.

v. *Enhanced microalgal carbon sedimentation.* While seagrass leaf litter is easily exported from the originating bed, the seagrass canopies enhance microalgal carbon sedimentation from the overlying water column by reducing flow over the bed (Gambi et al., 1990; Gacia and Duarte, 2001). This augments the labile carbon supply to the sediment.

In conclusion, the algal-based detrital pathway could be a major mechanism for carbon and energy transfer to upper trophic levels in seagrass-dominated ecosystems. Seasonal studies identifying the source of bacterial carbon are needed in order to provide a robust annual estimate of the relative contributions of the various sources of carbon. Such studies should be complemented with other studies focusing on the dynamics of the bacterial populations associated to the decomposing material. Estimates of bacterial activity and production would help to support the hypothesis of seagrass-dominated ecosystem being fueled via the detrital pathway (see discussions in Kenworthy et al., 1987 and in Velimirov and Walenta-Simon, 1993; Fig. 7, bottom).

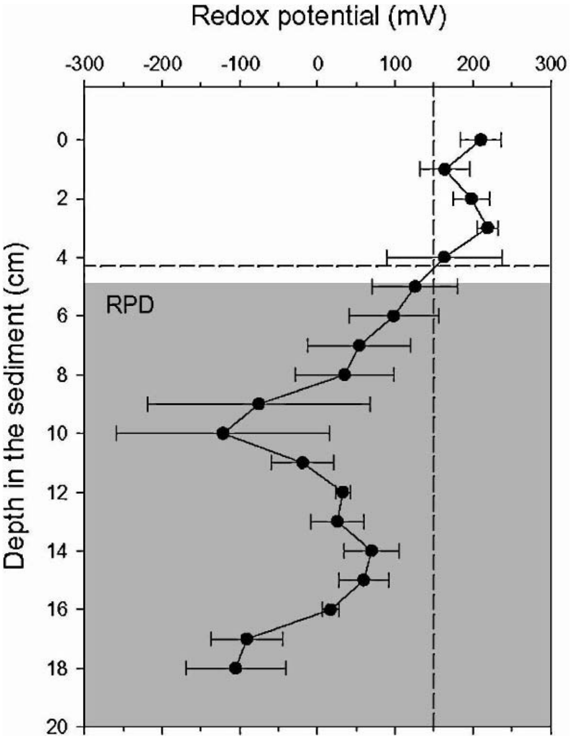

Fig. 10. Sediment average redox potential measured in a *Posidonia oceanica* meadow off Medes Islands (NW Mediterranean, Spain). The dashed lines cross to show the depth in the sediment where a redox potential of 150 mV is attained. The shaded area starts at the redox potential discontinuity (RPD). Error bars represent the standard error of the mean of six redox profiles (redrawn from Mateo, submitted).

2. Nutrients and Food Web Dynamics: Isotope Addition Experiments

Stable isotope studies have identified the benthic algae as the primary carbon source in some seagrass systems. However, it is still not known what factors determine the relative importance of phytoplankton, seagrass, and benthic micro- and macroalgal production in trophic dynamics. Fry et al. (1987) hypothesized that nutrient availability may determine which primary producers supply the bulk of the organic matter to food webs, suggesting that, under eutrophic conditions, ample nutrients would foster extensive growth by the benthic microalgae and phytoplankton, leading to a food web driven by algal production. This prediction is supported by the responses of some primary producer to elevated nutrients (Short and Burdick, 1996; see also Walker et al., Chapter 23 and Ralph et al., Chapter 24). However, in view our lack of understanding of mechanisms that affect food web dynamics and the current threat of eutrophication to seagrass systems, it is essential that the much more thorough investigations be carried out.

The role of nutrients is also important because, with eutrophication, the growth of epiphytes and phytoplankton are favored at the expense of seagrass production, typically resulting in the loss of seagrass cover at high nutrient inputs when phytoplankton and epiphytes shade out seagrass systems (Kemp et al., 1983; Borum, 1985. However, the effects of nutrients on epiphytes and phytoplankton are complex (see Borowitzka et al., Chapter 19 and Walker et al., Chapter 23). Analyzing the isotopic compositions of seagrass residents under various nutrient regimes may permit identification of differences in the flow of N and C through the food web, as changes in the nutrient dynamics may be expected to cause shifts in the relative contribution of organic matter by various primary producers to higher trophic levels. The isotope addition experiments magnify differences in the isotopic composition among producers and allow better resolution of C and N flows from primary producers to consumers (Peterson et al., 1985, 1993). Employing an experimental manipulation to generate distinct δ^{15}N values for seagrass and its epiphytes, Winning et al. (1999) were the first to use isotope additions. By adding ^{15}N-enriched potassium nitrate to mesocosms containing *Z. marina* and its epiphytes, they were able to produce significantly changed δ^{15}N values for these two primary producers. This demonstrated the potential of manipulating isotope values in the field to resolve trophic relationships and such an approach can actually solve another serious problem that limits the use of δ^{15}N as a tracer of organic matter through simplified food webs in mesocosms studies (see next three paragraphs).

Fry et al. (1987) observed that the sulfur and carbon isotopic compositions for consumers and their diets were similar, but the δ^{15}N values of consumers were on average 3.2‰ greater than that of their diet (as a consequence of excretion of ^{15}N-depleted nitrogen). In many subsequent studies, this average value was subtracted from consumers to infer potential diets; however, this practice is ill advised as the range of variation is very wide (from 0 to 6‰; Fry et al., 1987). While it is tempting to simplify, a careful study of seagrass associated food webs based on stable isotopes requires detailed knowledge of (i) fractionation phenomena associated with metabolic assimilation, (ii) seasonal variability in isotopic ratios, and (iii) variability in isotopic ratios between plant parts (see Vizzini et al., 2003 for the two last items).

Mutchler et al. (2004) have developed a field methodology for the isotope addition experiments, based on the mesocosm work of Winning et al. (1999). In these experiments, ^{14}N-labeled (i.e. ^{15}N depleted), slow-release fertilizer is used to both simulate eutrophication and generate differential isotopic compositions of *H. wrightii* and its epiphytes. After only 20 days of exposure to water column enrichment, the δ^{15}N values of the epiphytes were significantly different from those of the seagrass (−78‰ vs. −31‰, respectively, Fig. 11).

Although this methodology was developed to address food web dynamics under eutrophic conditions, the approach could easily be modified to generate isotopic tracers under ambient nutrient conditions. By actively 'labeling' organisms within seagrass beds, one can trace not only the flow of organic matter to higher trophic levels, but through creative isotope additions, investigate the degree of movement of 'labeled' organisms and assess the extent to which these organisms facilitate the retention or export of organic matter within and between seagrass beds and other habitats.

3. Partitioning of Ecosystem Autotrophic Components

There are a number of components of the seagrass food web that are often overlooked. For example, the extent to which food webs depend on locally-derived food resources vs. more transient planktonic resources needs to be quantified. Although locally-generated production is high in seagrass systems, organic matter flux through the planktonic and filter-feeding pathways may be significant as well. At another level, the relative contribution of the resident producers must be better understood. Until recently, the role of the sediment microalgae has been largely neglected (Fry et al., 1987), despite the fact that sediments within and between seagrass beds constitute a large area in the seagrass landscape (see Bell et al., Chapter 26). Broadly, the contribution of sediment microalgae within seagrass beds (∼18–35%) (see also Sections II.B and II.D.1) may be as great or greater than the contribution by the seagrass (∼24%), epiphytes (∼21%), and phytoplankton

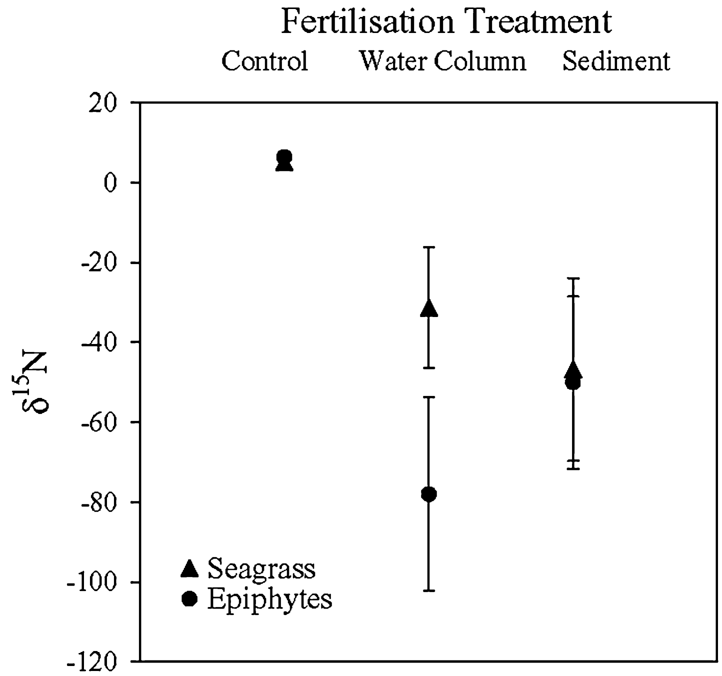

Fig. 11. $\delta^{15}N$ values (%, mean ±95% confidence intervals) of *Halodule wrightii* and epiphytic algae in seagrass beds exposed to control, water column, and sediment fertilization during 20 days (see text).

(~31%; averages calculated from a compilation by Daehnik et al., 1992).

4. From the Individual to the Landscape Level

Also overlooked in traditional studies of food web dynamics is the contribution of individual species in a community: measurements of primary production, biomass, and isotopic composition are often performed on samples containing complex assemblages of species, where the measurements integrate the functional properties as single points on a graph and ignore the individual contribution of each species. This practice is most common with microalgae and small invertebrates, both of which have been shown to be functionally important (Klumpp et al., 1992; Moncreiff et al., 1992). Although this 'guild-level' approach is a necessary starting point, much ecological information is lost when groups of species are combined; measuring the production, biomass, turnover time, density, consumption rate, and assimilation efficiency of individual species would permit quantification of the contribution by each species to the overall flux of matter within the system.

Addressing questions at larger scales is also possible: for example, in the trophic pathways between beds and other communities. Thus, stable isotopes will be useful in evaluating the residency time of individuals in particular beds (Fry et al., 2003). Knowing how organisms move between seagrass beds, unvegetated sediments, salt marshes, and other nearshore habitats as well as the degree to which they feed in each habitat will help to elucidate how organic matter production in these habitats is linked (see Valentine and Duffy, Chapter 20; Heck and Orth, Chapter 22; Kenworthy el al., Chapter 25; and Bell et al., Chapter 26). Landscape-level maps of production could be generated to relate areas of high productivity and carbon flux to landscape variables so that areas of greatest value to fisheries and the health of coastal ecosystems can be identified (see Bell et al., Chapter 26).

5. Stable Isotopes: Future Developments

A particularly strong approach for the future is a balanced combination of natural abundance analyses and isotope addition experiments. Natural abundance analyses can provide an assessment of the background conditions while creatively targeted isotope additions would afford opportunities to resolve trophic ambiguities, monitor changes in trophic dynamics in response to environmental factors (e.g. nutrient enrichment, fragmentation, and disturbance), or examine export of organic matter to other habitats. Despite the numerous difficulties of applying isotope additions in such open systems, advances continue to be made to permit isotope additions in the field. Along with direct isotope additions via spraying (Ottosen et al., 2001; Carman and Fry, 2002; Fry et al., 2003) or incorporation into fertilizer (Mutchler et al., 2004), organisms themselves could be labeled in the laboratory and 'released' into the field. Isotope signatures of specific beds (Stapel et al., 2001) or unvegetated sediments could be manipulated and the fate of the tracer monitored. Indeed, multiple isotope additions (e.g. ^{13}C, ^{15}N, and ^{34}S) may be applied (Carman and Fry, 2002).

E. Other Carbon Fates—Translocation and Seagrass Exudates

Retranslocation of carbon resources from senescent to young leaves, between above- and below-ground organs (e.g. Alcoverro et al., 2001) or between adjacent shoots (Marbà et al., 2002), are mechanisms apparently used by seagrasses for an efficient use of their resources. A maximum of 11% of the carbon gain by the *P. oceanica* leaves can be accumulated as non-structural carbohydrates in the whole plant (above- and below-ground organs, Alcoverro et al., 2001). The fraction of this amount that is actually stored in roots and rhizomes cannot be easily determined at this time due to different criteria by different authors concerning the size of the living below-ground compartment. The relevance of this possible fate for leaf carbon is also difficult to ascertain since the carbon accumulated during periods of positive plant carbon balance can be later mobilized to support the growth of new leaves during periods of negative plant carbon balance (Alcoverro et al., 2001). It has been shown that the use of stable isotopes may have a potential in the study of carbon reserves in seagrasses (see discussion in Vizzini et al., 2003).

Concerning clonal resource sharing, Marbà et al. (2002) found that from 27.1 to 80.6% of the carbon incorporated by the leaves of different seagrass species could be exported to adjacent shoots to contribute to the growth of new and colonizing shoots. For instance, the value estimated for *P. oceanica* was 26% in June at 11–15 m of depth (NW Mediterranean). During periods of reserve mobilization, carbon export to other shoots could be substantially higher. Since an asymmetrical transport between clones has been demonstrated (and not only in seagrasses) preferential transport of resources to pioneer ramets would, in effect, represent an important net carbon and nutrients loss from the source individuals.

Dissolved organic compounds have been recognized as a potentially important component of carbon transfer. In an early study, Moriarty et al. (1986) reported that the amount of dissolved carbon released into the water column by the leaves of *H. wrightii* was 1% of the carbon fixed. Carbon exuded from roots and rhizomes into the sediments was estimated as 6–17% of the ^{14}C fixed by the leaves. Leaf uptake, translocation to roots and rhizomes, and exudation into the sediment occurred within 6 h. Using two different methods to determine bacterial production, Moriarty et al. (1986) concluded that all the excreted ^{14}C was utilized by bacteria growing in the sediment. For the same species, Koepfler et al. (1993) found that dissolved inorganic carbon (DOC) concentration in pore-water was 25% higher in vegetated than in bare sediments. In *T. testudinum*, benthic net fluxes of DOC ranged from 0 to 216 mgC m^{-2} day^{-1} and were attributed mainly to seagrass exudation (Ziegler and Benner, 1999). Strong correlations between benthic DOC release and water column respiration suggested that water column heterotrophy was largely fed by seagrass exudation. Finally, an ecosystem model in Chesapeake Bay assigned to eelgrass-derived DOC an important role as a carbon source, accounting for up to 30% of littoral primary production (Buzzelli et al., 1998, 1999).

IV. Ecosystem Carbon Budgets and Carbon Sinks

The concept of ecosystem carbon budgets deserves a brief comment here to better focus the problem. Such a budget may compare the stocks of net or gross carbon incorporated by a producer compartment to the amount of carbon evolved from the detrital compartment during remineralization. Fates other than remineralization (such as grazing, export, and immediate release of DOC) need also to be known in order to account for all the carbon synthesized. Notice that ecosystem budgets can take into account (i) all producers of all compartments of the ecosystem, (ii) part of them, (iii) a single producer, or (iv) a part of a producer. The individual budget of a certain seagrass species can be largely positive, while growing in a globally heterotrophic ecosystem. It is suggested

Table 3. Summary of the annual budget and fate of leaf-derived carbon in *Posidonia oceanica* meadows in Medes Islands (Girona, Spain), the Bay of Calvi (Corsica, France), and Ischia Island (Naples, Italy). The values are the average for the range of depths indicated. The potential sink is the difference between leaf production and all known fates (remineralization, export and grazing). P:R accounts for the quotient between annual leaf net growth and leaf litter respiration. Values expressed in gC m^{-2} $year^{-1}$. The values in parentheses represent the percentage of annual leaf production (modified from Mateo, submitted).

	MEDES (5–13 m)	CALVI (1–30 m)	ISCHIA (5–20 m)
Production	153.5 (100)	155 (100)	96.9 (100)
Remineralization	61.3 (39.9)	68.7 (44.3)	23.2 (23.9)
Budget	92.3 (60.1)	86.3 (55.7)	73.7 (76.1)
Export	9.8 (6.4)	38.8 (25.0)	47.9 (49.5)
Grazing	10.0 (6.5)	31.0 (20.0)	6.3 (6.5)
Known fate	81.0 (52.8)	138.5 (89.3)	77.4 (79.9)
Potential sink	72.5 (47.2)	16.6 (10.7)	19.5 (20.1)
P:R	2.5	2.3	4.2

that these aspects be taken into account when interpreting budget results and comparing budgets from different studies.

A. Carbon Budgets

As mentioned in Section II.C, the available information on carbon budgets in seagrass beds comes from oxygen exchange experiments (Bay, 1982; Smith and Hollibaugh, 1997; Ziegler and Benner, 1998; Welsh et al., 2000). Almost all of these budgets provide global estimates for the ecosystem, distinguishing major compartments but without addressing the individual contribution of the different compartment components.

From Frankignoulle and Bouquegneau (1987) an annual P:R of 1.09 can be estimated for a *P. oceanica* bed in Calvi (Corsica, France). This would suggest that some seagrass beds, like coral reefs, are nearly in balance in terms of carbon balance. In a *Z. marina*-dominated bay (Tomales Bay, Ca, USA), Smith and Hollibaugh (1997) obtained a net heterotrophic carbon budget for the entire bay, with P:R = 0.9. They inferred that terrestrial and marine carbon sources each accounted for about half the heterotrophy of the system. Ziegler and Benner (1998), working in the seagrass-dominated Laguna Madre (Tx, USA) found that, while the water column was highly heterotrophic (P:R = 0.27), the benthos was net autotrophic with a P:R ratio of 1.16 (annual average). It was suggested that the benthos, dominated by *T. testudinum*, could be responsible for an important part of the heterotrophic activity of the water column and that this was a common situation for other temperate and tropical seagrass-dominated ecosystems (Ziegler and Benner, 1998, 1999 and references therein). In an intertidal *Zostera noltii* bed on the French Atlantic coast, Welsh et al. (2000) estimated a P:R of 1.6–2.8, values in the same order as those found in an earlier study in a *Halophila stipulacea* bed in the Gulf of Aqaba (P:R = 2.36; Bay, 1982). Clearly, we need more studies of whole seagrass beds to resolve the range of P:R ratios.

Currently, we also need to examine the carbon budget for individual components of the ecosystem to identify relevant factors governing the balance and to assess the relative contribution of each component (Kemp et al., 1997). In three *P. oceanica* beds encompassing depths from 0 to 30 m, the P:R ratio for leaves (net leaf production vs. leaf detritus respiration) ranged from 1.5 at the deep limit of plant distribution (in Medes Islands) to 4.9 at 10 m at Ischia Island (intermediate bed depth; see summary in Table 3). During 10 months of the yearly cycle studied in Medes Islands, the budget was positive (Fig. 12). This seasonal pattern is consistent with what is generally known of *P. oceanica* beds: plant productivity approaches its yearly minimum in late summer due to the greatest ambient nutrient deficiencies (Pirc, 1989; Alcoverro et al., 1997). Additionally, a massive leaf detachment takes place in late summer–autumn (Bay, 1984; Pirc, 1986; Romero et al., 1992; Mateo and Romero, 1997). These leaves enter the detrital compartment. Both meiofaunal and bacterial activity in this period of the year is high owing to the abundant fresh (nutrient-rich) organic matter available (López et al., 1995a,b; Danovaro, 1996; Mateo and Romero, 1997) and to the maximum annual water temperatures (23–25°C; Velimirov and Walenta-Simon, 1993). From the aforementioned,

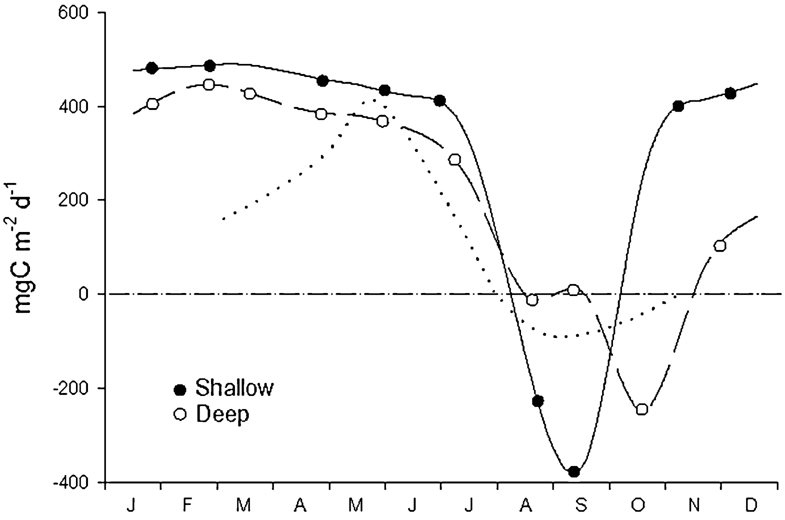

Fig. 12. Seasonal changes in *Posidonia oceanica* leaf carbon budget (Medes Islands, NW Mediterranean, Spain). The dotted line is the carbon budget estimated by Frankignoulle and Bouquegneau (1987) also for *P. oceanica* (Bay of Calvi, Corsica, France) assaying DIC and O_2 evolution within benthic chambers. The budget in Medes was estimated for the shallow and deep limits of plant distribution (from Mateo, submitted).

it appears that seagrass-dominated ecosystems are, with exceptions, somewhat autotrophic systems on an annual basis. However, as mentioned in Section II.B, it is often found that seagrasses are not the major contributors to this autotrophy. Based on these observations, several authors have suggested a structural rather than a trophic role for seagrasses (e.g. Frankignoulle and Bouquegneau, 1987, *P. oceanica* in Calvi, Corsica, France; Pollard and Kogure, 1993, *S. isoetifolium* in Dravuni Island, Fiji; Kaldy et al., 2002; *H. wrightii* and *T. testudinum* in Low Laguna Madre, Tx, USA).

B. Carbon Sinks

Once all the known fates of organic material have been accounted for, it is often found that there is an excess component, which is put down to refractory carbon. When the latter material is buried, it is in a highly decay-resistant chemical form, and the term 'refractory accumulation' has become widespread.

Information on burial of refractory carbon is very limited since the estimates available for seagrasses are indirect. Often refractory carbon is taken as deriving from below-ground organs, since leaf-derived carbon has a low residence time in the detrital compartment. However, a pool of refractory carbon originating from seagrass leaves has been found to be potentially very important as a short-term sink (see below).

Depending on the species, the time span for below-ground detritus to reach the refractory phase may range from a few months (e.g. eelgrass, Kenworthy and Thayer, 1984) to several years (e.g. Neptune grass, Romero et al., 1994). Degradation of refractory detritus occurs at a very slow rate and it may take many years, even millennia, to get measurable degradation (Mateo and Romero, 1997; Mateo et al., 1997). The following classification is proposed in order to provide some unifying guidelines when addressing the phenomenon of refractory accumulation. Two time scales are considered:

Short-term accumulation or sink refers to the pool of carbon that remains in the organic form after the first year (plant life cycle) of decomposition. In relation to the annual ecosystem budget, this pool has not been remineralized and hence represents a net accumulation. The residence time of this sink is therefore longer than 1 year and shorter than 2 or 4–6 years for above- and below-ground production, respectively (see below). The organic carbon in this sink is still susceptible to biological degradation processes. Assuming a steady-state for carbon accretion into this pool, the size of this sink should remain constant over time periods relevant to the biology of the plant.

Long-term accumulation or sink accounts for material with a biomass and nutrient content (C/N ratio) that no longer exhibit a change with time. In the best documented case, long-term accumulation of *P. oceanica* applies only to the carbon derived from below-ground organ production, starting 4–6 years after tissue death and lasting for decades, centuries, or millennia (Romero et al., 1994; Mateo and Romero, 1997; Mateo et al., 1997). The dynamics of this long-term sink is only affected by geochemical diagenetic phenomena. In the biospheric context, these kinds of sinks are usually named 'reservoirs' because they are considered virtually permanent. For periods comparable to a plant's biological cycle, this sink would increase in size.

1. Keys Processes for Material Accumulation

There is general agreement that the two main factors leading to an accumulation of carbon in sediments are (i) incorporation of carbon into refractory geomacromolecules or humic substances and (ii) oxygen availability (turnover) in the sediments (e.g. Henrichs, 1992, 1993). This means on the one hand, that carbon trapped in seagrass sediments does not necessarily have to be highly refractory provided the redox potential of the sediments is low enough, and on the other hand, that highly refractory material can remain intact even in oxidizing environments. A number of biological and environmental agents will modulate the extent of these two factors.

2. Chemistry of Refractory Material

Among all vascular plant components, lignin is considered to have the highest preservation potential (Klap, 1997 and references therein). The presence of this polymer in aquatic plants seems largely unnecessary and in fact, of all aquatic plants, seagrasses are the only ones that contain lignin (Lewis and Yamamoto, 1990; Kuo and den Hartog, Chapter 3). One possible reason is the terrestrial origin of seagrasses (Larkum and den Hartog, 1989), allied to the fact that decay-resistant material is useful at the leaf base and in rhizomes.

Despite the pioneering studies of Klap (1997) and Klap et al. (2000), in *P. oceanica*, the importance of lignin in making seagrass below-ground organs particularly decay-resistant still needs to be adequately addressed.

Evidence suggests that one cause for the refractory accumulation of seagrass below-ground detritus could be the progressive impoverishment of nutrients in the detritus and resulting slower decomposition (Melillo et al., 1984; Romero et al., 1992; Mateo and Romero, 1997; Sterner and Elser, 2002). López et al. (1998) found that in several *P. oceanica* beds in the NW Mediterranean, fertilization significantly increased bacterial activity. They found that in the fertilized plots, organic matter content was reduced by about 33% with respect to the controls, which suggested a potential role of nutrients.

The increasing tannin content of seagrass material during aging (Pergent, 1987) has also been proposed as another important factor that impairs microbial activity (Crouzet, 1984). Also, it has been demonstrated that this secondary compound can act against herbivory either by deterring herbivores or by reducing total protein availability (e.g. Robbins et al., 1987; Bernays et al., 1989).

3. Redox Potential and Anoxia

Anoxic conditions and oxidation reduction (redox) potential in sediments may also play a role in preservation of refractory carbon (Harrison, 1989). However, this is the subject of much current debate. For instance, it is known that many bacteria that possess cellulase activity seem to be strict anaerobes (Kenworthy and Thayer, 1984; Roth and Hayasaka, 1984) and numerous studies have reported partial or complete lignin degradation by both aerobic and anaerobic decomposers (Klap, 1997 and references therein). In two reviews of the topic, Henrichs and Reeburgh (1987) and Henrichs (1993) conclude that organic matter decomposition rates are not substantially different under oxic or anoxic conditions. The situation is obviously complicated by the fact that seagrass sediments are highly structured with a variety of different environments (Kristensen, 2000).

Lepidochronological dating (i.e. dating rhizome remains from the number of leaf bases present), elemental analysis, and sediment redox measurements provide evidence suggesting an important role of anoxia in helping to retain the organic carbon from below-ground production (Mateo, submitted). In a *P. oceanica* bed, the redox potential discontinuity (RPD) was found to be located at 5 cm from the sediment surface (range 4–6 cm, in March) which is close to the 150 mV of redox potential limit (Fig. 10), i.e. the potential at which it is assumed that sediments are reduced and therefore bacterial efficiency for remineralization drops drastically (e.g. Stumm and Morgan, 1981; Kristensen, 2000). From the fact that t, the elongation rate of recent rhizomes was found to be 0.95 cm yr^{-1} and this must be matched by the sediment accretion rate, since the rhizomes do not become exposed, it can be estimated that a reducing environment will arise within 5–7 yr; at which point decay rates would fall drastically. From Mateo and Romero (1997) the C:N ratio of dead rhizome sheaths stabilizes at $\sim$6 yr, which may well be the result of anoxia and changed redox conditions. Although the foregoing suggests that anoxia and redox potential in seagrass sediments promotes organic matter preservation, the considerable amount of contradictory evidence makes it advisable to further investigate the effect of oxygen depletion on below-ground refractory material.

4. Other Factors

The situation is made more complex by the influence of other factors especially the four following ones, which clearly favor low redox potential in marine sediments and therefore help material preservation: (i) high temperatures, (ii) high organic supply, (iii) low water motion, and (iv) small sediment grain size.

It has been repeatedly demonstrated that high temperatures increase bacterial activity in seagrass sediments (e.g. López et al., 1995a,b; Mateo and Romero, 1997) with concomitant oxygen consumption. On the other hand, low temperatures may promote material accumulation by reducing bacterial activity. In terrestrial ecology, it is well established that cold biomes present the largest accumulation of organic matter in the soil as a consequence of reduced decomposition rates (e.g. Swift et al., 1979).

An abundant organic matter supply not only from seagrass production but from micro- and macroalgal detritus (Section II.D.1) accelerates oxygen depletion in the sediment.

Reduction of water velocity over a bed due to water friction of the seagrass canopy (Gambi et al., 1990; Koch et al., Chapter 8) leads to seagrass vegetated areas having a sediment retention capacity up to 15 times higher than barren areas (Gacia et al., 1999) and accelerates burial. Also, low water motion and a small grain size of the sediment lead to a reduction of pore-water renewal and oxygenation, very effectively helping to maintain a low redox potential in the sediment.

Finally, Cebrián et al. (2000) examined the formation refractory material throughout the development of *C. nodosa* beds and found that refractory accumulation increased from small patches, to large patches, to climax beds.

C. Refractory Carbon: The Potential Seagrass Carbon Sink

Refractory accumulation has two main consequences for the ecology of seagrass beds. First, the capacity of climax beds to sequester organic carbon is indicative of their role as sinks in oceanic and global models. Second, the accumulation of refractory detritus entails a loss of nutrients from the bed since a significant amount of nutrients remain bound to fibrous compounds (i.e. lignin, cellulose) in the detritus (Romero et al., 1994; Mateo and Romero, 1997; Mateo et al., 1997). Hence, refractory accumulation also needs to be added to the export of dead leaves out of the bed when estimating the bed's total dependence on imported nutrients. Yet, despite its importance, refractory accumulation is clearly the least studied of all the routes of seagrass production listed in Eqs. (1) and (2).

Information on organic matter burial in seagrass sediments began to be studied in detail during the 1990s, and the only direct estimations available so far are basically limited to the below-ground-derived production of the species *P. oceanica* (Romero et al., 1994; Mateo et al., 1997, 2002; Mateo, submitted). The two different time scales for seagrass carbon sinks, described at the beginning of this section, will be distinguished below.

1. Short-Term Sinks (i.e. Material Broken Down Over a Period of a Year or so)

The preliminary compilation made for this chapter showed that the percentage of seagrass production accumulated as refractory material varies from ca. 1 to 62% and the absolute value from 3 to 207 gC m^{-2} year^{-1} (Fig. 3G and H). The studies on *P. oceanica* presented in this chapter (for beds off the islands of Medes, Calvi, and Ischia; Table 3) and estimates from two other available studies (Cebrián et al., 1997; Gacia et al., 2002), indicate that the average potential carbon sink (short-term) from leaf-derived material for this species can be estimated as

Table 4. Estimates of the potential annual carbon sink in *Posidonia oceanica* meadows and other environments in absolute values and relative to net primary production (% NPP; adapted and simplified from Mateo, submitted). Estimates are presented separately for leaves, below-ground organs, total plant and total ecosystem (see text for details).

		Potential sink	
	Depth (m)	gC m^{-2} $year^{-1}$	% NPP
Posidonia oceanica			
Aboveground			
Medes	5	123	59
Medes	13	22	23
Calvi	20	17	11
Cala jonquet	4	66	17
Fanals point	15	40–55	36–50
Ischia	5–20	20	20
Average	12	57	29
Range	4–20	17–123	17—59
Belowground			
Short-term			
Medes	5	84	91
Medes	13	24	96
Long-term	5–20	9–112	4–51
Total plant			
Medes	5	207	63
Medes	13	46	42
Ischia	5–20	58	43
Total ecosystem			
Fanals point	15	182	43
Calvi	20	56	45
Others			
Peatlands	–	26–99	14–52
Coastal areas	–	62	50
Oceanic areas	–	0.02–4	0.01–2
Seagrass ecosystems	0–40	3–182	1–62

57 gC m^{-2} $year^{-1}$ (ranging 17–123 gC m^{-2} $year^{-1}$) representing 29% of the annual leaf production (17–59%, Table 4). This estimate accounts for a substantial part of the range estimated for all seagrasses, suggesting that the phenomenon of refractory accumulation may present large between- and within-species variability.

As discussed above, carbon from below-ground organs may also contribute to the sediment refractory pool. The carbon stored in a *P. oceanica* bed after the first year of decay (short-term sink) was estimated to be 84 and 24 gC m^{-2} $year^{-1}$ at the shallow and deep limits of the bed, respectively (Mateo and Romero, 1997); this represents 91 and 96% of the total below-ground production, respectively (Table 4). Adding up both above- and below-ground sinks for the *P. oceanica* bed in Medes Islands, the total potential sink for the studied year amounted to 207 and 46 gC m^{-2} $year^{-1}$ at 5 and 13 m, respectively (63 and 42% of total plant production, Table 4). Comparable estimates were only possible for the bed in Ischia Island that yielded an average of 58 gC m^{-2} $year^{-1}$ (43% of total plant production; average for 5–20m depth).

2. Long-Term Sinks (i.e. Accumulations Over a Period of 4 to Many Years)

The accumulation of refractory organic matter in below-ground deposits is a phenomenon exclusive to a very few species in the biosphere. Ecosystems dominated by peat lands (e.g. Gorham, 1991; Clymo, 1992), mangroves (e.g. Macintyre et al., 1995; Middleton and Mckee, 2001), and seagrasses (Lipkin, 1979, *Thalassodendron ciliatum*; Shepherd and Sprigg, 1976, *Posidonia australis* and related species; Boudouresque et al., 1980; Romero et al., 1994 and Mateo et al., 1997, *P. oceanica*) are, to our knowledge, the only plants generating important refractory deposits with a very high residence time (from decades to millennia). The long-term below-ground carbon stocks of peat lands are well studied, with estimates up to 12 × 10^4 gC m^{-2} (e.g. Warner et al., 1993). This value falls well within the average range, obtained for several *P. oceanica* deposits (usually known as 'mattes') studied by Mateo et al. (1997), of 4–16 × 10^4 gC m^{-2}. Long-term annual carbon burial rates are also similar for peat lands and *P. oceanica* below-ground deposits, 26–99 gC m^{-2} $year^{-1}$ and 9–112 gC m^{-2} $year^{-1}$ (Table 4), representing 14–52% and 17–59% of the production, respectively.

The reason why *P. oceanica*, and possibly *P. australis*, seem to be the only seagrasses that form such thick long-term organic reservoirs (at least 5 m thick, Fig. 13), lies most likely in the combination of the multiple factors: (i) a low palatability of the below-ground tissues, (ii) the fact that sheaths remain attached after leaf-blade abscission, (iii) the increasing concentration of highly refractory carbon compounds (e.g. lignin; Klap et al., 2000) and herbivore deterrents (Crouzet, 1984) during tissue aging, (iv) the long life span of this species, (v) the rapid burial capacity promoted by high sedimentation rates enhanced by reduced water velocity, and (vi) the low redox potential maintained by (a) an intense organic matter accretion, (b) a relatively high bacterial activity, and (c) a low hydraulic

Fig. 13. A reef-like formation of *Posidonia oceanica* 'matte' of the island of Formentera (Balearic Islands, Spain). The millenary accumulation of *P. oceanica* detritus derived from its below-ground organs (roots and rhizomes) results in the elevation of the sea bottom forming a highly organic sediment that resembles terrestrial peat formations. In the upper part of the picture, the living shoots of *P. oceanica* can be recognized. The matte in the picture is more than 5 m high (photograph by M. San Félix).

conductivity of the sediment. All these factors converge to make a substantial part of *P. oceanica* below-ground detritus unavailable for decomposers.

Applying a model proposed by Clymo (1984) for terrestrial peat, the residence time of the *P. oceanica* matte has been estimated between 2800 and 12,500 years (Mateo et al., 1997, 2002). This old continuous organic reservoir constitutes a unique feature in the marine environment. Apart from its implications in the context of biospheric carbon sinks (Smith, 1981), it should be regarded as a valuable repository of paleo-ecological information of a seagrass ecosystem during, at least, the second half of the Holocene (Mateo et al., 2002).

V. Summary and Future Work

A. Production

Together with coral reefs, mangrove forests, and some macroalgae, seagrass beds are responsible for some of the most productive and complex marine ecosystems. They show highly variable above-ground production rates ranging from 0.003 to 15 gDW m^{-2} day^{-1} (0.1 to 18.7 gC m^{-2} day^{-1}) with average values probably around 1–2 gC m^{-2} day^{-1}. More recently, it has been demonstrated that below-ground production can be as substantial as 50% of total plant production, although covering a wide range from 0.001 to 20 gDW m^{-2} day^{-1} (carbon content in below-ground tissues is still too scattered to attempt an estimate).

The increasing number of different methods currently coexisting to measure seagrass production points to the need for an intense effort of exploration of new approaches able to provide accurate values.

It is becoming clear that seagrass productivity is not always the major contributor to secondary production in seagrass ecosystems; the few reports available seem to place seagrasses as a lesser contributor (24–38%), exceeded by benthic macroalgae (33–42%), and seagrass epiphytes (20–60%)

and with sediment microalgae apparently sometimes accounting for the highest part of the productivity (18–56%). Areas which need much attention are the role of below-ground parts as producers, consumers or storage organs, canopy structure, and light dynamics.

B. Fate

The preliminary review attempted in this chapter shows that overall, most seagrass production is decomposed within the bed (∼65%) while the rest is exported (∼15%), grazed (<10%), or accumulates in a refractory pool (∼10%). Detritus nutrient content may be a controlling factor on decomposition rates, alongside the oxygen status of the sediment. The importance of certain chemical constituents (e.g. lignin and tannins) of seagrass detritus in influencing microbial attack still needs to be explored in almost all seagrass species.

Seagrass leaf nutrient content and the intensity of herbivory is a controversial topic and studies are needed of how different field spatial (i.e. cultivated patches vs. entire beds) and temporal scales (i.e. seasonality) affect the relationship. Along with these manipulations, specific assimilation rates for the major grazers need to be determined because most grazing rates given in the literature may represent large overestimates of the actual carbon flux from producers to consumers.

Given our lack of understanding of mechanisms that affect food web dynamics and the current threat of eutrophication to seagrass systems, it is recommended that the role of nutrients in determining the fluxes of carbon and nitrogen be investigated. Both surveys of natural abundances of stable isotopes and isotope addition experiments will be useful in these investigations.

The lack of a method that adequately covers the entire ecosystem and integrates export rates over time has been identified as the main reason behind the scarcity of export estimates.

C. Budgets and Sinks

Based on the relatively limited information available, seagrass ecosystems appear to be net producer systems, with P:R ratios ranging from 1 to 4.9; this range is mainly a consequence of the quantitative importance of export and refractory accumulation and needs detailed investigation. If true, it would confirm the role of seagrass-dominated areas as food sources for downstream ecosystems. At the same time, we need more efforts to study single ecosystem components to avoid losing important information of bed functioning.

The percentage of the production accumulated as refractory materials has often been shown to be modest; however, the high productivity of seagrasses results in a substantial absolute amount of carbon fluxing to this pool. In the context of a world with an increase in atmospheric CO_2, global estimates suggest that seagrass ecosystems may be relevant carbon sinks, not only at a local scale, but also in a biospheric context; 0.08 PgC year^{-1}, representing 20% as much as for phytoplanktonic communities.

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Chapter 8

Fluid Dynamics in Seagrass Ecology—from Molecules to Ecosystems

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I. Introduction

Fluid dynamics is the study of the movement of fluids. Among other things, it addresses velocity, acceleration, and the forces exerted by or upon fluids in motion (Daugherty et al., 1985; White, 1999; Kundu and Cohen, 2002). Fluid dynamics affects every aspect of the existence of seagrasses from the smallest to the largest scale: from the nutrients they obtain to the sediment they colonize; from the pollination of their flowers to the import/export of organic matter to adjacent systems; from the light that reaches their leaves to the organisms that live in the seagrass habitats. Therefore, fluid dynamics is of major importance in seagrass biology, ecology, and ecophysiology. Unfortunately, fluid dynamics is often overlooked in seagrass systems (Koch, 2001). This chapter provides a general background in fluid dynamics and then addresses increasingly larger scales of fluid dynamic processes relevant to seagrass ecology and physiology: molecules (μm), leaves and shoots (mm to cm), seagrass canopies (m), seagrass landscapes (100–1,000 m), and seagrasses as part of the biosphere (>1,000 m). Although gases are also fluids, this chapter is restricted to water (i.e. compressed fluids), how it flows through seagrasses, the forces it exerts on the plants, and the implications that this has for seagrass systems. Seagrasses are not only affected by water in motion, they also affect the currents, waves and turbulence of the water masses surrounding them. This capacity to alter their own environment is referred to as “ecosystem engineering” (Jones et al., 1994, 1997; Thomas et al., 2000). Readers are also encouraged to consult a recent review by Okubo et al. (2002) for a discussion on flow in terrestrial and aquatic

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vegetation including freshwater plants, seagrasses, and kelp.

II. Fluid Dynamics: Fundamentals

The general aspects of water flow in aquatic systems can be understood through a number of fluid dynamic concepts that have been developed largely for steady state conditions, i.e. when there are no temporal fluctuations in the water flow (Fischer et al., 1979; White, 1999; Kundu and Cohen, 2002). In the absence of motion, seawater is described by: (i) density (ρ, i.e. mass/volume), which is used preferentially over mass (m) in fluids; (ii) kinematic viscosity (ν) which is a measure of how easily the fluid will flow (i.e. $\nu = \mu/\rho$, where μ is the molecular or dynamic viscosity); and (iii) hydrostatic pressure (p), which is a function of the depth from the water surface (i.e. $p = \rho g z$, where g is the acceleration due to gravity and z is the depth—note that the depth can be the distance from the water surface to the seafloor or the height from the seafloor to the water surface; see below). The introduction of energy into a fluid causes fluid motion, and the motion in natural systems is generated by pressure gradients ($\mathrm{d}p/\mathrm{d}z$) as result of gradients in water surface elevation or depth ($\mathrm{d}z/\mathrm{d}x$; where x is the horizontal distance) and/or density ($\mathrm{d}\rho/\mathrm{d}z$). The major source of this energy input is the sun, which causes winds that lead to changes in surface elevation (i.e. $\mathrm{d}z/\mathrm{d}x$; waves, currents, and seiches in embayments), and thermal gradients (i.e. $\mathrm{d}\rho/\mathrm{d}z$) that lead to expansion, instabilities, and mixing. Other sources include inputs of freshwater and other chemical constituents (i.e. $\mathrm{d}\rho/\mathrm{d}z$), tides and currents due to gravitation and acceleration of the earth-moon and earth-sun systems (i.e. $\mathrm{d}z/\mathrm{d}x$), and the Coriolis force due to the earth's rotation (i.e. $\mathrm{d}z/\mathrm{d}x$) (Kundu and Cohen, 2002).

The flow in seawater is described with respect to a fixed Cartesian reference frame (Eulerian perspective) with x defining the principal flow direction, y defining the cross-stream direction, and z defining the vertical direction. Whereas it is common in geophysics to define z as the depth (i.e. with respect to the water surface), it is equally appropriate and perhaps more informative to use height (i.e. defined with respect to the seafloor) as the vertical direction (e.g. Ackerman and Okubo, 1993). The volume flow rate (Q), as defined by the velocity (u) of the fluid that passes through a given cross sectional area A (which is usually defined with respect to the x and y; i.e. $\mathrm{d}x\mathrm{d}y$), is conserved because seawater is an incompressible fluid. This continuity principle is one of the essential elements of fluid dynamics, which, among other things, is used to determine mass balances of water-borne materials (e.g. Hemond and Fechner, 1994). The flow of water leads to a second type of pressure, the dynamic pressure ($p = {}^{1}/_{2}\,\rho u^2$), which, when added together with the hydrostatic pressure, is constant along a flow streamline (i.e. Bernoulli's principle).

Abbreviations
A – cross sectional area
C – celerity or phase velocity of waves
C_d – drag coefficient
C_s – concentration on the seagrass surface
C_w – concentration in the water column
D – molecular diffusivity
D – depth
DBL – diffusive boundary layer
δ – diffusive boundary layer thickness
δ_D – diffusive boundary layer (=DBL)
δ_I–inertial sublayer or logarithmic (log) layer
δ_v–viscous sublayer
F_d – friction or viscous drag
F_p – form or pressure drag
g – acceleration due to gravity
H – water depth
H – wave height
h – canopy height
J – flux
κ – von Karman constant
l – length scale
λ – wavelength
m – mass
μ – molecular or dynamic viscosity
p – hydrostatic or dynamic pressure
Q – volume flow rate
ρ – density
REI – relative wave exposure index
Re – Reynolds number
Re_crit – critical Reynolds number
St – Stanton number
T – wave period
τ – shear stress
τ_o – boundary shear stress
τ_W – wall shear stress
u – current velocity
u_* – friction velocity
U_k – critical velocity
U_o – free stream velocity
ν–kinematic viscosity
x – horizontal distance
x – principal flow direction
y – cross-stream direction
z – vertical direction or depth
z_o – roughness height

Bernoulli's principle, which states that the sum of the hydrostatic pressure and dynamic pressure along a streamline are constant (Vogel, 1994), helps to explain flow-induced pressure changes (i.e. lift) that occur within, around, and under seagrass canopies (e.g. Nepf and Koch, 1999). Drag is another important force that acts downstream of obstacles. It has two additive components: (i) the friction or viscous drag that exists due to the interaction of the obstacle's surface with the water, which can be defined algebraically (i.e. $F_\mathrm{d} = {}^1\!/_2 C_\mathrm{d} \rho A u^2$, where C_d is the drag coefficient, a shape and flow dependent constant); and (ii) the dynamic, form or pressure drag (F_p) that exists under high flows when flows separate from boundaries, which cannot be expressed algebraically and must, therefore, be determined empirically. As u increases, the dynamic drag contributes a disproportionate fraction of the total drag. It is important to note that drag is a force that operates opposite to the flow direction in that it "sucks" a moving object upstream or a stationary object downstream.

Water flow can exhibit a number of different properties that depend on the temporal and spatial scales under investigation. Water flow could either be smooth and regular as if the fluid flows in layers (i.e. laminar flow) or rough and irregular as if the flow is "chaotic" (i.e. turbulent flow). This depends on the velocity and the length scale (i.e. temporal and spatial scale, respectively) under investigation as defined by the Reynolds number ($Re = lu\rho/\mu$ or more simply $Re = lu/\nu$; where l is the length scale appropriate for the hypothesis being tested). *Re*, which is the non-dimensional ratio of inertial to viscous forces in a fluid, defines four regimes that grade into one another: (i) creeping flow ($Re \ll 1$), which occurs at very low flows and spatial scales such as those experienced by individual bacteria cells; (ii) laminar flow ($1 < Re < 10^3$) as defined above; (iii) transitional flow ($Re \sim \mathrm{O}(10^3)$; i.e. of the order of 10^3), which involves the production of eddies and disturbances in the flow and is characterized by a critical *Re* (Re_crit) defined for a particular geometry and flow; and (iv) fully turbulent flow ($Re \gg 10^3$). Associated with these flow patterns are important differences related to the fluid dynamic forces (e.g. friction vs. pressure drag) and mass transfer processes (diffusion vs. advection) that operate under the different regimes (see below; White, 1999; Kundu and Cohen, 2002). Moreover, because *Re* is scale dependent, it is possible to experience multiple flow regimes simultaneously in the flow field depending on the spatial scale under investigation. Consequently, flow is almost always turbulent at large spatial scales such as seagrass beds, but it can also be laminar on the scale of seagrass leaves and flowers (e.g. Ackerman and Okubo, 1993; Koch, 1994). This not-so-subtle distinction can influence the application and interpretation of physiological and ecological processes in seagrass canopies (see Section III).

As indicated above, the flow conditions become more complicated when water approaches a boundary (e.g. seagrass canopy, leaves, or seafloor, depending on the scale) or any obstacle for that matter. The water cannot normally penetrate boundaries, except for the most porous ones (see reviews in Boudreau and Jørgensen, 2001; Okubo et al., 2002), and more importantly, the water molecules directly next to a boundary stick to the boundary rather than slip by it. This no-slip condition leads to the development of a velocity gradient perpendicular to the boundary (Fig. 1), as the velocity at the boundary will be zero relative to the free stream velocity (U_0). As the water flows downstream, the velocity gradient will grow in size and a slower moving layer of fluid will develop next to the boundary, which is referred to as the boundary layer under turbulent conditions, otherwise technically it is a deformation layer (Prandtl and Tietjens, 1934). This boundary layer, which is defined by velocities $<0.99\ U_0$, has a thickness of δ that is relatively small and can be expressed as a function of *Re* and x. Initially it appears laminar in nature, but the boundary layer will become turbulent when the local *Re* ($Re_x = ux/\nu$) approaches a critical value of 3 to 5×10^5, in the case of a flat plate oriented parallel to the flow. In nature, this transition is accelerated by the presence of roughness or obstacles on the boundary (Schlichting, 1979; Nikora et al., 2002; Fig. 1) including undulations on macroalgal blades (Hurd and Stevens, 1997). In addition to the streamwise structure in a fully developed boundary layer, there is important vertical structure as well. The first layer directly adjacent to the boundary is the viscous sublayer ($\delta_\mathrm{v} \approx 10\nu/u_*$ where u_* is the friction velocity, which is a velocity scale that provides an indication of the mass transfer within the boundary layer) in which the forces (or stresses if surface forces are considered) are largely viscous, and consequently the mass transfer in this layer is slow and dominated by diffusion, especially within the thin diffusional sublayer (also called the diffusive boundary layer; DBL) at the bottom of this

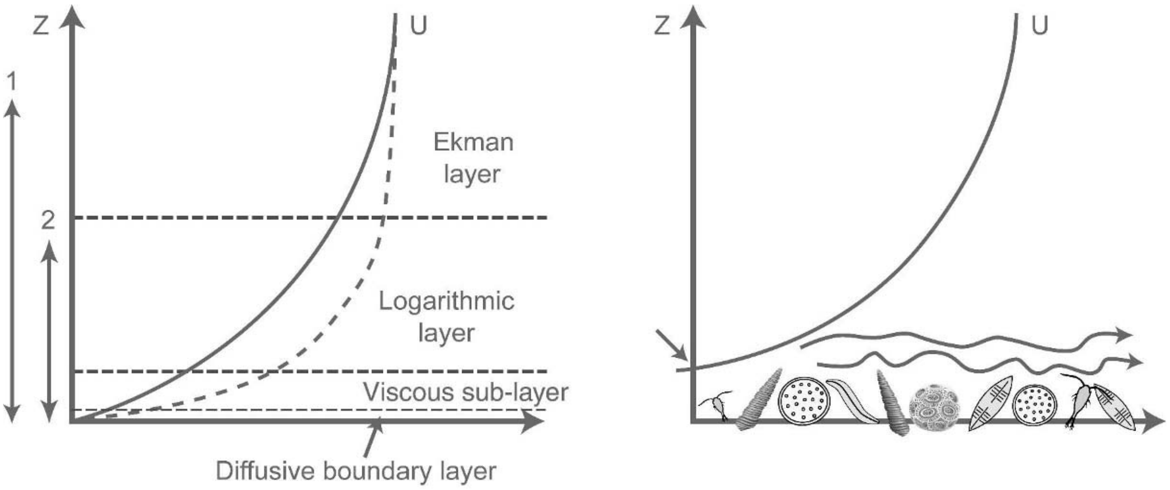

Fig. 1. Velocity (U) gradient/profile adjacent to smooth (left) and rough (right) boundaries. Weak currents (solid line) generate a relatively thick boundary layer (1) when compared with boundary layers (2) generated by faster currents (dashed curve). Names of boundary layer zones are provided for the fast flowing water velocity profile. When the boundary (such as a seagrass leaf) is rough (e.g. due to the presence of epiphytic organisms), a roughness height (arrow) extends the boundary layer farther into the water column. Consequently, the flux of nutrients and carbon from the water column to the boundary is reduced.

layer ($\delta_D \approx \nu/u_*(\nu/D)^{-a}$, where D is the molecular diffusivity and a is a constant equal to 1/2 or 1/3; (Lorke et al., 2003). It is important to note that $\delta_D \ll \delta_v$, which relates to the fact that the molecular diffusion of momentum (i.e. $\nu \sim 10^{-6}$ m^2 s^{-1}) is much larger than the molecular diffusion of a scalar quantity like CO_2 (i.e. $D \sim 10^{-9}$ m^2 s^{-1}). The next layer is the inertial sublayer or logarithmic (log) layer ($\delta_I \approx 0.15\delta$), which is a region of exponentially increasing velocity; hence, it is dominated by inertial forces (or stresses) and mass transfer occurs through turbulent advection. The outer layer of the boundary layer is the largest layer, and it represents a transition to the free stream flow (it is referred to as the Ekman layer in situations where the Coriolis force causes rotation of the flow; Fig. 1). Boundary layers exist embedded in one another as they are defined by spatial scale (e.g. Ackerman, 1986; Boudreau and Jørgensen, 2001); consequently, it is possible to define boundary layers around plant epiphytes, flowers, leaves, canopies, and the benthos. In this sense, there is a benthic boundary layer (BBL) above the seagrass canopy, and separate boundary layers around individual shoots, leaves, flowers, and the smaller constituents described above. In addition, it is important to note that there may also be boundary layers generated by other types of water motion (e.g. wave current boundary layers), but this topic is beyond the scope of this review. For biologically relevant information on this topic see Denny (1988).

Another important consequence of the no-slip condition at a boundary is the tractile or shearing force that the boundary imparts on the fluid, which is a tangential force causing rotation of the fluid next to the boundary. A boundary or wall shear stress (τ_0 or τ_W) is defined as the quotient of the shearing force and the area of the boundary, and $\tau_W = \mu du/dz$ within the viscous (or laminar) sublayer and $\tau_W = \rho u_*^2$ in general. In practice, it is difficult to measure the shear force or the aerial extent of the boundary or to apply the algebraic relationships, and thus a number of methods have been developed to measure τ directly using force balances in flow chambers or indirectly using velocity gradients based on the law of the wall ($u = u_*/\kappa \ln(z/z_0)$, where $\kappa = 0.4$ is the von Karman constant, and z_0 is the roughness height; see Fig. 1; for a review of techniques and references for the measurement of bed shear stress see Ackerman and Hoover (2001). The velocity gradient method involves applying the law of the wall to the velocities measured in the log layer of the boundary layer. In this case, u_* is equal to κ multiplied by the slope of the linear regression of velocity on the natural logarithm transformed distances from the boundary, and z_0 is equal to e raised to the value of the x intercept of the same regression. This method has been applied successfully above and within seagrass canopies (e.g. Fonseca and Fisher, 1986; Gambi et al., 1990; Ackerman and Okubo, 1993). It is important to note that other engineering models have been applied to rough canopies such as corals and seagrasses with the direct measurement of canopy friction and the use of the Stanton number, *St* (uptake rate by the surface/advection over the surface), to determine the efficiency of canopy uptake (e.g. Thomas et al., 2000; Thomas and Cornelisen, 2003). Reconfiguration of seagrass canopies under higher flow conditions (e.g. Fonseca et al., 1982; Ackerman, 1986), and/or unsteadiness due to *monamis* (waving of the canopy; see Section V.C) caused by an instability of the mean velocity profile (Ackerman and Okubo, 1993; Ghisalberti and Nepf, 2002) and waves (Koch, 1996; Koch and Gust, 1999) represents a challenge to researchers. Even so, τ is the preferred form (over u) of expressing hydrodynamic conditions near boundaries (leaves, flowers, sediment etc; see Nowell and Jumars, 1984).

Hydrodynamic conditions in the environment are rarely stationary, especially in wave-dominated seagrass habitats where a more appropriate characterization of the fluid environment is that it varies in a periodic fashion with each passing wave. Waves represent the movement of energy through a fluid and exhibit a periodic motion, especially when viewed at an interface (e.g. the water surface). In this case, the passing wave (crest followed by trough) causes a submersed object on the surface to move in a circular or orbital fashion, the diameter of which is equal to the wave height (H). The orbital motions also extend downward through the fluid in a series of orbitals that diminish in diameter with depth until a depth (z) of $1/2\lambda$ (where λ is the wavelength) is reached.

The classification of waves can be based on the disturbing force that creates them, the restoring force that destroys them, and their wavelength (Garrison, 2000). The disturbing force is the source of energy that causes the wave, which can be (i) wind stress acting on water surface causing capillary and gravity waves, (ii) the arrival of surge or sea wave causing swell, (iii) wind setup in an embayment creating seiches, (iv) a change in atmospheric pressure causing short-lived storm surge, and (v) large disturbances (landslides, volcanic eruptions, earthquake) that cause seismic waves (or tsunami; the so-called tidal waves that are actually due to gravitational inertial forces). The restoring forces that reduce the disturbance to the water surface include (a) surface tension due to the molecular cohesion of water molecules, which works for small waves (i.e. λ <1.73 cm; capillary waves) and, (b) gravity that operates on larger waves (i.e. $\lambda \gg 1.73$ cm). Whereas the wavelength can be used to distinguish differences among the smallest of waves, it really provides a measure of wave size and relationship to energy; the smaller the wavelength, the higher the energy. Some typical relationships include (1) wind waves (λ <60–150 m), (2) seiches (λ is large and a function of the basin size), (3) seismic waves (λ <200 km), and (4) tides ($\lambda = 1/2$ circumference of earth; note that tides are caused by gravity and inertia).

Seagrasses experience each of these types of waves, but the most common are wind waves, swell, and tides (tides can be viewed as long waves). Wind waves develop from capillary waves to gravity waves as a function of the wind strength and direction and the fetch (length of the unrestricted zone over which the wind stress operates). Wind waves are affected by local wind conditions, and are generally of a short period, T (T is time it takes for a wave to pass a fixed point). Wave action has a direct impact on the ecosystem, with obvious effects on sediment transport, boundary layer processes and physical stresses (Denny, 1988; Koch and Gust, 1999). There has also been some suggestions that fetch (relative wave exposure index) is an important factor affecting seagrass on a landscape level (e.g. Fonseca and Bell, 1998; Hovel et al., 2002; Krause-Jensen et al., 2003).

Just as the size of the wave is determined by the wavelength, the shape of the orbit is determined by the water depth. In deep water (i.e. $z > 1/2\lambda$) the orbits are circular, whereas in shallow water (i.e. $z < 1/20\lambda$) the orbits become elliptical or flatter due to the influence of the bottom. Intermediate waves (i.e. $1/20\lambda < z < 1/2\lambda$) are more complicated as they combine characteristics of deep and shallow water waves. Deep water waves travel at a celerity or phase velocity $C = \sqrt{g\lambda/2\pi}$ or λ/T ($\sim$1.56 T), but shallow water waves are slower due to the influence of the bottom and travel at $C = \sqrt{gz}$ (or $3.1\sqrt{z}$), which is why waves build up in shallow areas (Denny, 1988). Waves travel in a wave train, which is a progression of groups of waves of similar λ from the same origin. Energy is lost by the leading wave, which eventually dissipates, but a new trailing edge wave is created from this energy. In deep water, the waves progress with $C \propto \lambda$ but the wave train has a group velocity of $C \propto 1/2\lambda$, whereas in shallow water the celerity of the individual waves slow until the wave and group celerities are equal. It is important to note that waves and wave trains are not isolated from one another; circumstances can lead to destructive interference with calm periods between wave trains and constructive interference with the generation of large waves including rogue wavees due to the convergence of many waves.

As indicated above, a number of changes occur as waves enter the nearshore and ultimately reach the shore. The waves become shallow water waves as the wave train encounters the friction (shear stress) of the bottom or seagrass canopy, the wave orbits become more elliptical in shape near the bottom, and the wave crests become more pronounced. This can lead to wave-induced transport in a process referred to as Stokes drift, which may be of considerable importance in many coastal environments (Monismith and Fong, 2004). The steepness of the wave becomes unstable if it is greater than 1:7 (H:λ) and the water at the crest begins to travel faster than the water near the bottom and it will break into a plunging wave, spilling wave, or surging wave depending on the steepness and topography of the bottom. Since waves approach the shore at different angles, they are unlikely to break simultaneously and may refract from the original direction leading to the complexity of waves experienced in coastal seagrass beds (Koch and Gust, 1999). Realistically, the fluid dynamic conditions within these nearshore regions are affected by a number of factors including tides and wind waves, all of which lead to significant changes in the surface elevation and water flow within seagrass beds. The general predictions are that seagrasses, like other benthic vegetation, increase the bottom shear stress and hence have a wave dampening affect (see Section **V**.B., below). This process has been relatively well characterized for coastal kelp forests (see review in Okubo et al., 2002), but has yet to be examined in a thorough manner for seagrasses. Clearly, additional efforts are needed in this area.

Whereas, the ultimate goal of studying fluid dynamic concepts is to better understand ecological processes in seagrasses, it is important to note that vegetative flows remain the most complex and difficult flows to describe and understand (Raupach et al., 1991; Finnigan, 2000). Therefore, applications in vegetated flows have typically involved steady state condition (i.e. non turbulent), although some progress in unsteady flows has been made with respect to seaweeds (Gaylord and Denny, 1997). Fortunately, this realization provides a challenge to those interested in the biological, chemical, geological, and physical processes that occur in seagrass systems.

III. Micro-Scale Processes at the Molecular Level (μm)

As water flows through seagrass beds, a boundary layer develops on the sediment surface as well as on each seagrass component exposed to the moving water (leaf, short-shoot, flower) (Ackerman, 1986; Fonseca and Kenworthy, 1987; Koch, 1994; Cornelisen and Thomas, 2002). The faster the water moves, the thinner the diffusive boundary layer (DBL, or δ_D) becomes (Massel, 1999; Fig. 1) and, consequently, the faster the transfer of molecules from the water column to the sediment and/or seagrass. It follows that when currents are weak, the flux of molecules to the seagrass surface may be limited by diffusion through the δ_D (i.e. physical limitation). Under those conditions, many biological sites or enzymes in the seagrass tissue are available to assimilate molecules when/if they reach the plant's surface (Koch, 1994; Cornelisen and Thomas, 2002). After a critical velocity (U_k) is reached (Fig. 2), the transfer

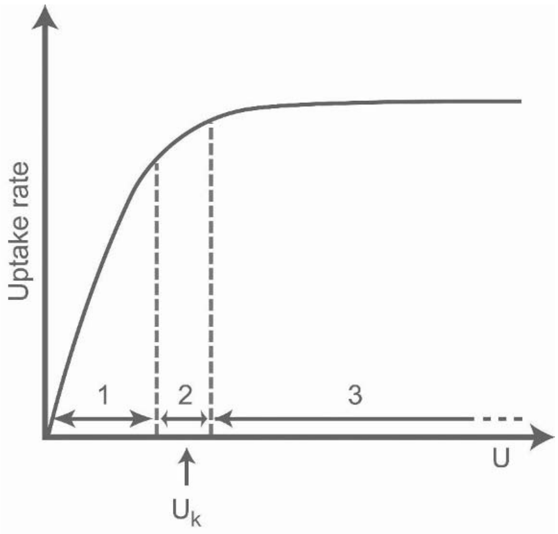

Fig. 2. An example of uptake kinetics by seagrass leaves exposed to increasing current velocities (U). U_k is the critical current velocity at which uptake rate saturates (equivalent to I_k in photosynthesis x irradiance curves). At currents below U_k (1), uptake is mass transfer-limited and at currents above U_k (3), uptake is kinetically limited. A combination of both limitations may occur at flows around U_k (2). If nutrient concentration in the water column increases, the curve is likely to shift upwards. Additionally, other types of responses to water flow are also possible (see text).

of molecules through the δ_D is no longer the limiting factor. Instead, the capacity of biological uptake sites or enzymes to assimilate molecules that reached the plant surface becomes limiting (Koch, 1994). In this case, the conditions are said to be kinetically (and not physically) limiting. When velocities are at intermediate levels, around U_k, a combination of physical (δ_D) and kinetic (enzymes) limitations may influence the uptake of nutrients (Sanford and Crawford, 2000). At velocities below 3–5 cm s^{-1} (U_k), photosynthesis (i.e. carbon uptake) in *Thalassia testudinum* and *Cymodocea nodosa* is δ_D limited, whereas at velocities above U_k, photosynthesis seems to be limited by the kinetics of Rubisco (Koch, 1994). Interestingly, a similar U_k value was found for the kelp *Macrocystis integrifolia* (Stevens and Hurd, 1997). In contrast, some seagrass studies were unable to detect a kinetic limitation in the assimilation of nutrients in flowing water (i.e. no U_k), instead, assimilation was δ_D limited up to the maximum velocity tested: 20 cm s^{-1} for *Thalassia testudinum* and its epiphytes (Cornelisen and Thomas, 2002) and 34 cm s^{-1} for *Zostera marina* (Fonseca and Kenworthy, 1987). This difference may be due in part to experimental conditions. Specifically, studies in which assimilation was only a function of velocity were performed with entire plants rooted in sediment and covered by epiphytes, while the experiments in which assimilation was a function of velocity and enzyme kinetics were done with epiphyte-free leaves, in the laboratory. For further discussion of the role of diffusive boundary layers on photosynthesis, see Larkum et al., Chapter 14.

Mass transfer to seagrass leaves does not only depend on the velocity and δ_D thickness but also on: (1) the thickness of the periphyton layer (complex of debris, mucus, bacteria, algae, small animals, and sediment particles) on the seagrass leaves (Jones et al., 2000), (2) the reactions occurring within the periphyton layer (Sand-Jensen et al., 1985; Jones et al., 2000; Cornelisen and Thomas, 2002) and (3) the concentration of the molecules in the water column adjacent to the seagrasses-periphyton complex (Sanford and Crawford, 2000). The water interstitial to the periphyton is expected to be static (with the exception of occasional sweep events; Nikora et al., 2002); therefore, δ_D increases linearly with periphyton thickness (Jones et al., 2000). Consequently, the spatial scale for diffusion of molecules from the water column to the leaf surface is longer and δ_D-limited conditions are more likely to occur. The critical δ_D thickness at U_k has been estimated to be 98 μm and 280 μm for periphyton-free leaves of *Cymodocea nodosa* and *Thalassia testudinum*, respectively (Koch, 1994), whereas the δ_D on artificial leaves with periphyton was quantified to be 950 μm in thickness (Jones et al., 2000). The δ_D limitation of molecules such as nitrogen, phosphorous and carbon may be further exacerbated by the reactions occurring within the periphyton layer. Epiphytic algae tend to assimilate biologically important molecules before they reach the seagrass surface (Jones et al., 2000; Sanford and Crawford, 2000; Cornelisen and Thomas, 2002), thereby competing for vital nutrients (Sand-Jensen et al., 1985). If the uptake kinetics of epiphytes is more efficient than that of seagrasses, the microalgae could potentially outcompete the seagrasses in the uptake of nutrients (including carbon) from the water column (Sand-Jensen et al., 1985; Beer and Koch, 1996; Cornelisen and Thomas, 2002). According to Fick's first law:

$$J = D\frac{C_w - C_s}{\delta_D}$$

where J is the flux of molecules, C_w the concentration in the water column, and C_s the concentration on the seagrass surface. δ_D limiting conditions become less important as the concentration of nutrients (C_w) in the water column increases (i.e. eutrophication). Under such eutrophic conditions, uptake is controlled by the kinetics of periphyton and seagrasses (Sanford and Crawford, 2000). As a result, one can hypothesize that as coastal waters become more eutrophic, mass transfer-limitations may become less important to seagrasses, but this is a complex process as the growth of the epiphytes as a function of the nutrient concentration also needs to be taken into account. Additionally, when uptake rates are δ_D limited, kinetic processes become less important and the uptake rates become a function of the planar area of seagrasses and epiphytes exposed to water flow.

As indicated above, the Stanton number (*St*), a dimensionless number, can also be used to quantify the efficiency of a seagrass canopy to remove nutrients from the water, as it is the flux of a chemical to a surface divided by its advection past the surface (e.g. Thomas et al., 2000). *St* can be obtained via direct measurements of nutrient uptake and velocity measurements, or can be calculated.

The calculated values have not always matched the measured values possibly due to the dependence of *St* on the friction coefficient (Thomas et al., 2000), a parameter that decreases as the seagrass canopy bends when exposed to increasing velocities (Fonseca and Fisher, 1986). Additionally, the *St* only parameterizes the transport into the canopy, i.e. it parameterizes the flux across the interface defined by the top of the canopy, not the diffusive sub-layers on individual leaves.

The discussion of fluxes of inorganic nutrients through the DBL so far assumed steady state flows. In nature, the thickness of the δ_D tends to fluctuate over time and space (Koch, 1994). Wave-induced oscillatory flows and/or large-scale turbulent eddies tend to disrupt the δ_D for short periods of time (fractions of a second) during which the δ_D is stripped away and the supply of molecules near the blade surface is replenished (Nikora et al., 2002). If these pulses of enriched water near the seagrass leaf occur on a regular basis such as under wave-dominated conditions, the flux of nutrients to the plant surface is expected to be enhanced (Stevens and Hurd, 1997). As indicated in Section II, little is currently known about the physiological implications of δ_D fluctuations on seagrass leaves.

IV. Processes at the Shoot Level (mm–cm)

When considering the hydrodynamic forces exerted on an individual seagrass shoot, the entire canopy (group of shoots) needs to be taken into consideration. The canopy tends to attenuate currents and waves thereby reducing the forces exerted on individual shoots. Even at the edge of the canopy, seagrass shoots may be sheltered to a certain extent by the presence of adjacent shoots (Granata et al., 2001). It follows that the biomechanical properties of seagrass shoots (a response to the forces exerted on them) are also altered by the canopy characteristics and the capacity of the canopy to attenuate currents and waves. Therefore, a feedback mechanism is expected between seagrass shoots, canopies, and the fluid forces that act on them.

A. The Role of Fluid Dynamics in Epiphytic Growth on Seagrass Shoots

Epiphytes growing on seagrass leaves are commonly related to the nutrient concentrations in the water column (Frankovich and Fourqurean, 1997). Epiphyte levels are even used as indicators of eutrophication (Stankelis et al., 2003). Unfortunately, little is known about ecological factors (other than light and nutrients) that regulate epiphytic growth on seagrass leaves (Pinckney and Micheli, 1998; see also Borowitzka et al., Chapter 19). Due to the lack of data on the effect of currents on seagrass epiphytes, one can only speculate that epiphyte biomass should increase proportionally with water flow as a result of decreased mass transfer limitation (e.g. Cornelisen and Thomas, 2002). But the interaction between the grazing community and water flow also needs to be taken into consideration as strong currents (and/or high waves) may eliminate grazers allowing more epiphytes to grow under strong flow conditions (an indirect effect of water flow on epiphytes; Schanz et al., 2002).

Only a few studies have evaluated the effect of waves on epiphytic loading on seagrass leaves. Although no difference was found in total epiphyte biomass in a wave-exposed and a sheltered seagrass habitat (Pinckney and Micheli, 1998), it seems that the composition of the epiphytic layer is responsive to water flow. Diatoms, coralline, and some filamentous algae dominate under wave-exposed conditions, while blue-green and other filamentous algae dominate under calm conditions (Kendrick and Burt, 1997; Pinckney and Micheli, 1998). This difference has been attributed to the size of the epiphytes on seagrass leaves (i.e. the influence of drag).

Natural fluctuations in water flow also affect the epiphytic community. If an epiphytic community develops during relatively calm conditions, species with high drag (i.e. large area exposed to the flow) may become dominant, but if the flow increases over a short period of time (e.g. storms), these epiphytes are then removed (Cambridge, 1979; Biggs, 1996).

B. Hydrodynamic Forces Exerted on Shoots and Shoot Biomechanics

Our knowledge of the forces exerted by flowing water on seagrass shoots or the biomechanical properties of seagrass shoots is very limited. We know that most seagrasses tolerate a wide range of water motion, from stagnant water to relatively high velocities ($100\ \mathrm{cm\ s^{-1}}$, Phillips, 1980; Dierssen et al., 2003). In the short-term (minutes), this is likely due to their capacity to bend as the velocity increases thereby minimizing drag (by minimizing the leaf area exposed to the flow; Sand-Jensen, 2003). Reproductive shoots of *Zostera marina* were found to be approximately one order of magnitude stiffer than macroalgae but two to three orders of magnitude less stiff than trees (Patterson et al., 2001), allowing seagrass shoots to bend and, as a result, minimize drag (Fonseca et al., 1982; Sand-Jensen, 2003). In a terrestrial grass (*Arundinaria tecta*), the sheath contributed 33% of the overall bending stiffness (Niklas, 1998). Perhaps the sheath surrounding the base of seagrass shoots also increases the bending stiffness of seagrass shoots making them stiffer than macroalgae. In the long term (weeks), seagrasses likely acclimate to water flow through growth changes in anatomy and morphology such that drag, breakage, and dislodgement are minimized. Eutrophication has been shown not to alter the tensile strength that *Zostera marina* leaves can withstand (Kopp, 1999). Another aspect to be considered in the estimation of the drag exerted on seagrass shoots is the epiphytes that colonize their leaves. Epiphytes on a red alga (*Odonthalia floccosa*) increased the drag exerted on the macrophyte (Ruesink, 1998). It is likely that this would also happen with epiphytes on seagrass shoots.

The risk of being dislodged due to excessive drag is highest during storm events when waves and currents are at their maximum ($F_\mathrm{d}\ \alpha\ u^2$). Massive loss of *Zostera marina* is expected when currents reach values above 4 m s^{-1} (Kopp, 1999). One mechanism to cope with this risk seems to be the existence of a few strong (reproductive) seagrass shoots that can resist extreme events and protect the other shoots in a population (Patterson et al., 2001). Within a population, vegetative male shoots of *Phyllospadix torreyi* tended to be dislodged at lower flows than the female plants (Williams, 1995).

The forces exerted on seagrasses exposed to waves are more complex than those in unidirectional flows. As water in waves accelerates in different directions during the course of each wave, organisms exposed to such unsteady flows are subjected to acceleration reaction forces as well as drag (Koehl, 1984). These forces are higher than in unidirectional flows at the same instantaneous velocity (Koehl et al., 1991) and the maximum drag occurs at a different time than the maximum acceleration reaction forces. In these wave-swept environments, a long flexible shape (Fig. 3) can minimize the forces exerted on the anchoring system (roots in the case of seagrasses). This is confirmed by the finding that leaves of *Posidonia australis* become longer as wave exposure increases (Larkum, 1976). The long leaves tend to move in one direction during the passage of a wave. If the leaves begin to move in the other direction before they are fully extended (Fig. 3), they will sway back and forth with the waves without imposing too much drag on the roots (Koehl, 1984).

C. Water Flow Around Seagrass Shoots—Ecological Implications

Seagrass shoots are obstructions to flowing water. When considering the vertical scale, seagrass shoots are exposed to a gradient of velocities in the canopy and benthic boundary layers. Due to the no-slip condition, the slowest flows are found near the sediment surface and the strongest flows near the top of the canopy. As a result of this vertical difference in velocities and the horizontal differences in upstream versus downstream velocities around a shoot, a vertical pressure gradient develops on the downstream side of the seagrass shoot: high pressure near the bottom where the currents are relatively slow and low pressure farther up in the water column where currents are stronger. This leads to the development of significant ascending flows (i.e. as high as 15% of ambient) immediately downstream of seagrass shoots (Fig. 4; Nepf and Koch, 1999). Pressure gradients around shoots (Huettel and Gust, 1992) can also lead to the intrusion of water into permeable sediments upstream of the shoot (high pressure zone; Koch and Huettel, 2000) and porewater upwelling downstream of the shoot (low pressure zone) (Nepf and Koch, 1999). For example, around a single *Thalassia testudinum* shoot exposed to a current speed of 10 cm s^{-1}, water was found to penetrate 2.5 cm into the permeable sediments (Fig. 4); a depth an order of magnitude larger than that affected by diffusion (Jørgensen and Boudreau, 2001). This flow-induced intrusion of water into seagrass-colonized permeable sediments may bring organic particles (Huettel et al., 1996) closer to the root zone and remove toxic compounds from the sediments such as sulfide (Koch, 1999a). Most of the impact of water intrusion into the sediment occurs over the first 6 h which coincides with semi-diurnal tides (Koch and Huettel, 2000). Therefore, the exchange between the sediments and the water column seems to be maximized in seagrass habitats in which the current direction changes every 6 h.

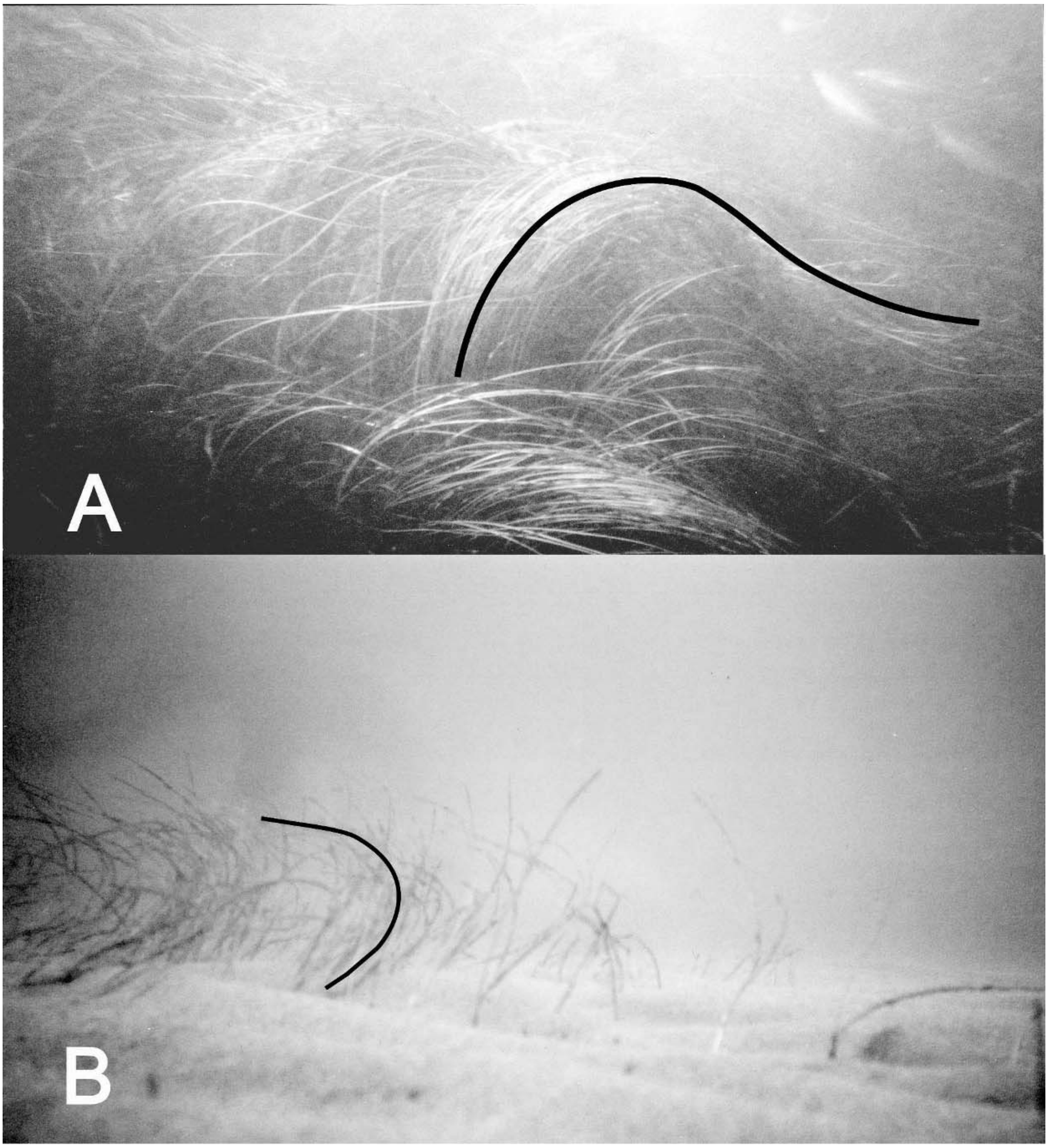

Fig. 3. Waving of seagrass leaves in wave-dominated habitats: (A) *Phyllospadix torreyi* at approximately 2.5 m depth at Punta Morro, Pacific coast of Mexico and (B) *Halodule wrightii* at approximately 1 m depth, north of Placencia, Belize. The lines were traced over individual leaves in order to emphasize the bending pattern. Note that the leaves are continuously moving back and forth every few seconds with the passage of waves. Photos: E.W. Koch.

The combination of the pressure-induced upwelling of porewater and the vertical ascending flows immediately downstream of the seagrass shoots colonizing permeable sediments appear to generate a slow “stream” connecting the sediment porewater and the water column at mid-height in the seagrass canopy (Nepf and Koch, 1999; Fig. 4). Under these circumstances, exchanges between the sediment

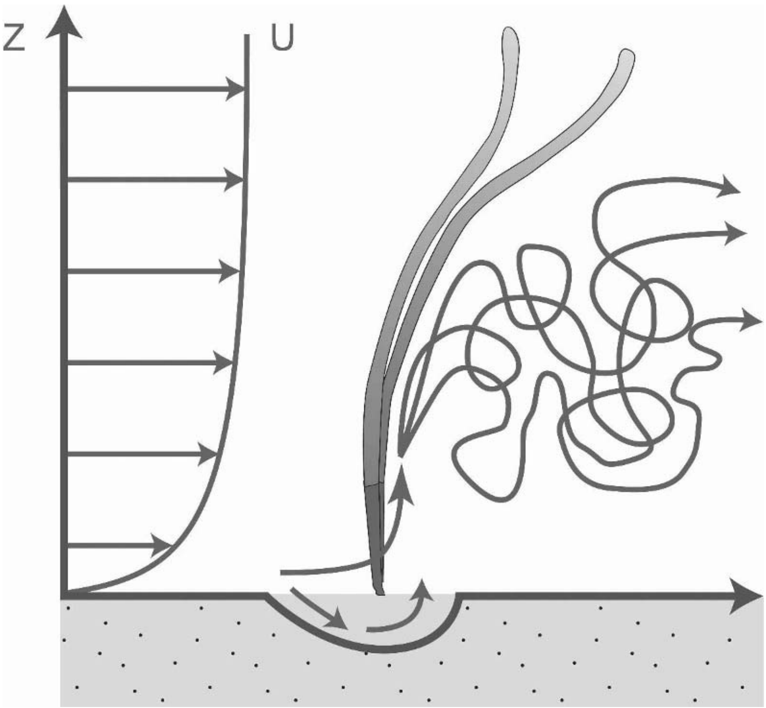

Fig. 4. Vertical ascending flows and porewater flows generated by pressure gradients around a seagrass shoot. As seagrass shoots live in the benthic boundary layer (see velocity (U) profile on the left), the top of the shoot experiences faster velocities and lower pressure than the bottom of the shoot. As a result, a vertical ascending flow is generated downstream of the shoot. This water then disperses horizontally at the point where the leaves bend over with the flow. Due to the pressure gradients generated on the sediment surface when the flowing water impacts the seagrass shoot, water also penetrates into permeable sediments leading to a zone in which the porewater is washed out by the overlying water. Z, distance above the sediment interface. Modified from Nepf and Koch (1999) and Koch and Huettel (2000). It is possible that the upwelling porewater may be transported high into the water column via the above processes.

porewater and the water column are not driven by diffusion but by advection (Huettel and Webster, 2001). This process could benefit the seagrasses by bringing recently remineralized nutrients and carbon to seagrass leaves (Nepf and Koch, 1999).

D. The Role of Fluid Dynamics in Seagrass Reproduction

Pollination in water (hydrophily) is uncommon in angiosperms, and restricted mostly to the monocotyledons, including the seagrasses (Les et al., 1997; Ackerman, 2000, Chapter 4, this volume). It is relevant to contrast seagrass with their freshwater relatives. Pollination in freshwater plants involves pollen or detached-floating anthers contacting the stigmas of floating or partly submerged carpellate flowers/inflorescences or submerged pollen "showering" (sedimenting) to stigmas from elevated anthers (Arber, 1920; Sculthorpe, 1967; Cook, 1982). Pollination in seagrasses, however, involves pollination underwater (i.e. hydrophily or submarine pollination), in which pollination occurs through the action of currents (Ackerman, 1995). In some cases (i.e. shallow seagrass populations that may be exposed to the air and the single species *Enhalus acaroides*), pollination may occur on the water surface (ephydrophily) when the pollen or stamens touch exposed stigmas (Cox, 1988). The concept that surface pollination (or pollination in two dimensions) was responsible for the evolution of seagrass pollination modes (Cox, 1988) is unsound because it assumes that pollen transport is random and, thus, recurrent, which is not the case, as wind generated movements are directional, not random (Ackerman, 1995).

Seagrasses possess a number of morphological features that appear to be associated with submerged or submarine pollination, notably their filamentous pollen shapes (Ackerman, 1995), which evolved convergently–multiple times in the Najadales and functionally in the Hydrocharitales (Pettitt, 1984; Ackerman, 1995, 2000). Pettitt (1984) reviewed the research pertaining to seagrass pollination biology, but that review was limited taxonomically with respect to pollen transport and capture mechanisms. The situation has improved, but remains largely limited to the mechanistic studies of submarine pollination in the north temperate species, *Zostera marina* (Ackerman, 1986, 1993, 1995, 1997a,b, and 2002). Fortunately, recent progress has been made with respect to other species including *Amphibolis antarctica* (Verduin et al., 1996), *Posidonia australis* and *Posidonia sinuosa* (Smith and Walker, 2002).

The mechanics of pollination in *Z. marina* were studied in a laboratory flow chamber using stroboscopic photography and in the field using physical models of pollen and adhesive surfaces deployed in the canopy (Ackerman, 1997a,b, 2002). Pollination was found to occur under laminar and relatively viscous conditions at the scale of flowers (i.e. low *Re*; see Niklas, 1992; Vogel, 1994), and was affected by the emergence of female flowers from within the inflorescence. The emergence of flowers (and other reproductive organs in subsequent phenological processes) led to an increase in the fluid shear stress (τ) in the local flow (Ackerman, 1997a), which caused the filamentous pollen (2.7 mm × 7.5 μm diameter) to rotate and cross streamlines toward female flowers (Ackerman, 1997b). The axial force responsible for the pollen motion varied directly with the length and aspect ratio of the pollen (Forgacs and Mason, 1958). Consequently, filamentous pollen need only be close to female flowers to pollinate by: (i) direct interception on stigmas; (ii) rotation within one half a pollen length of stigmas; and (iii) by being redirected through streamlines toward flowers (Ackerman, 1997b).

Ancestral spherical pollen, on the other hand, could only pollinate via direct interception due to the limited axial force exerted on the spherical-shaped body. Canopy flow conditions at the scale of leaves and flowers were laminar, which indicates that observations would be similar to those in the laboratory flow chamber (Ackerman and Okubo, 1993; Ackerman, 2002). Higher recovery of filamentous pollen models compared to spherical ones also supports the biomechanical model (Ackerman, 2002). Moreover, field observations of pollination in *Amphibolis* were consistent with the predictions from *Z. marina* (Verduin et al., 1996), as were results from *Posidonia* (Smith and Walker, 2002). It is important to note that seagrasses can maintain relatively high outcrossing rates through hydrophily (Ruckleshaus, 1995; Waycott and Sampson, 1997; Reusch, 2000; Waycott et al., Chapter 2). This is especially true for populations found under conditions that promote pollen dispersal, such as exposed bays (e.g. Waycott and Sampson, 1997). It is reasonable to conclude that the strong convergence of filiform pollen morphologies in seagrasses indicates a similar convergence in pollination mechanisms linked to fluid dynamics. Further research from a diversity of seagrass taxa will be needed to determine the validity of this statement.

Seed dispersal phenomena in seagrasses are somewhat analogous to pollination mechanisms in that they are poorly recognized but have become better understood in recent years (Van der Pijl, 1972; Orth et al., Chapter 5). This is in part due to the clonal nature of seagrasses in which rhizomatous growth, in addition to anchoring and binding of sediments, was viewed as the principal mechanism of population growth. However, the occurrence of annual populations (e.g. Keddy and Patriquin, 1978), colonization of new areas (e.g. Turner, 1983), and recovery from small and large-scale disturbances (e.g. Rasmussen, 1977; Inglis, 2000) via seeds has led to the realization that seed dispersal is important in this group.

There is considerable diversity in seed biology and ecology related to the polyphyletic nature of seagrasses (e.g. Les et al., 1997) and their evolutionary innovations. For example, 7 of the 12/13 genera of seagrasses have dormant seeds, with geocarpy (releasing seeds under the sediments) occurring in *Halodule, Cymodocea,* and *Halophila* (Inglis, 2000). Geocarpy appears to facilitate recovery from disturbances in *Halodule,* where dispersal involves near-bed saltational movements analogous to sediment transport, and high densities of seeds accumulate in dugong feeding depressions (Inglis, 2000). Other species, which have reproductive organs elevated above the seafloor, such as *Z. marina*, have small, negatively buoyant seeds that sink in still water, and that likely move on the order of 1–10 m horizontally in the water column, depending on the canopy flow (see Okubo et al., 2002). Sometimes seeds (5–13% of seeds in Long Island Sound) are released with a bubble of gas (presumably from the lacunar spaces in the infructescence), which can extend dispersal distances on the order of 10–100 m (Churchill et al., 1985). Longer distance dispersal

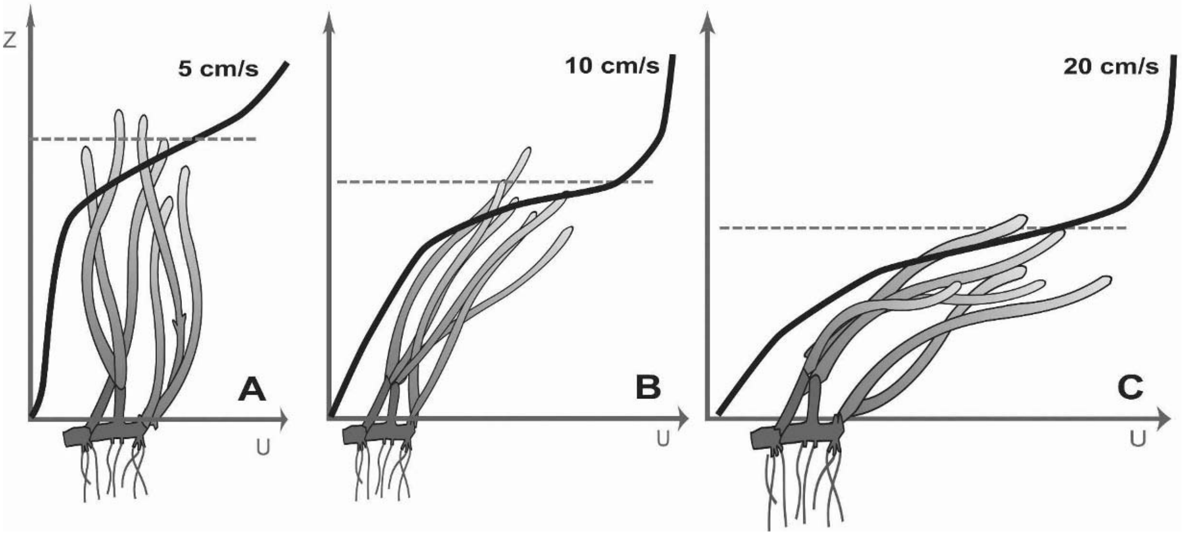

Fig. 5. Vertical velocity (*U*) profiles (thick solid lines) in seagrass canopies exposed to 5 cm s^{-1}(A), 10 cm s^{-1} (B) and 20 cm s^{-1} (C). *Z*, distance above the sediment interface. Note that, as velocity increases, the angle of bending of the canopy increases and the canopy height (dashed horizontal line) decreases. Based on a flume experiment using a short (16 cm) and dense (1,000 shoots m^{-2}) *Zostera marina* canopy (Gambi et al. 1990).

(e.g. 100 m–10 km) occurs through the floatation of buoyant diaspores (i.e. fruits and seeds) and detached infructescences and/or whole reproductive shoots, which "sweepstake" because of the positive buoyancy provided by the lacunar gas system (e.g. Harwell and Orth, 2002; Lacap et al., 2002; see review in Orth et al., Chapter 5). In the latter case, seeds may be released from the plant while it is floating, or when the plant reaches the shore. Lastly, seeds may be transported in the guts of birds, sea turtles, and fish (e.g. Baldwin and Lovvorn, 1994), leading to potentially large dispersal distances on the order of 100 m–1,000 km, especially in migrating birds.

It is interesting to note the morphological/ecological specializations that evolved in *Phyllospadix,* which is found in wave-exposed environments where it is a dominant successional species (Wyllie-Echeverria and Ackerman, 2003). In this case, dispersal is facilitated by wave action by an undescribed mechanism, but recruitment is limited to areas that have branching macrophytes with cylindrical thalli onto which the bifid, barbed fruits attach (Turner, 1983). This is a form of obligate facultative succession in that there is no recruitment in the absence of the correct type of turf-forming algae.

V. Processes at the Canopy Level (m)

Fluid dynamic processes at the canopy level are the most studied and best understood. Based on more than two decades of research, it is well-accepted that seagrass beds attenuate currents and waves and, as a result, tend to accumulate organic and inorganic particles as well as spores and larvae in the canopy. These concepts are now being refined and new questions linking water flow and seagrasses are being addressed. This section provides a general background on classical concepts and then focuses on new trends in fluid dynamics at the canopy level.

A. Attenuation of Currents by Seagrass Canopies: A Classical Concept

The presence of seagrass canopies in the benthic boundary layer (BBL) alters the roughness of the bottom (Fonseca and Fisher, 1986; Nepf and Vivoni, 2000; Granata et al., 2001). As a result, the vertical flow profile shown in Fig. 1 is altered (Fig. 5), especially when the plants occupy a large portion of the water column, i.e. when H/*h* <10 (H is the water depth and *h* the canopy height; Nepf and Vivoni, 2000). Reduced flows are common within the canopy

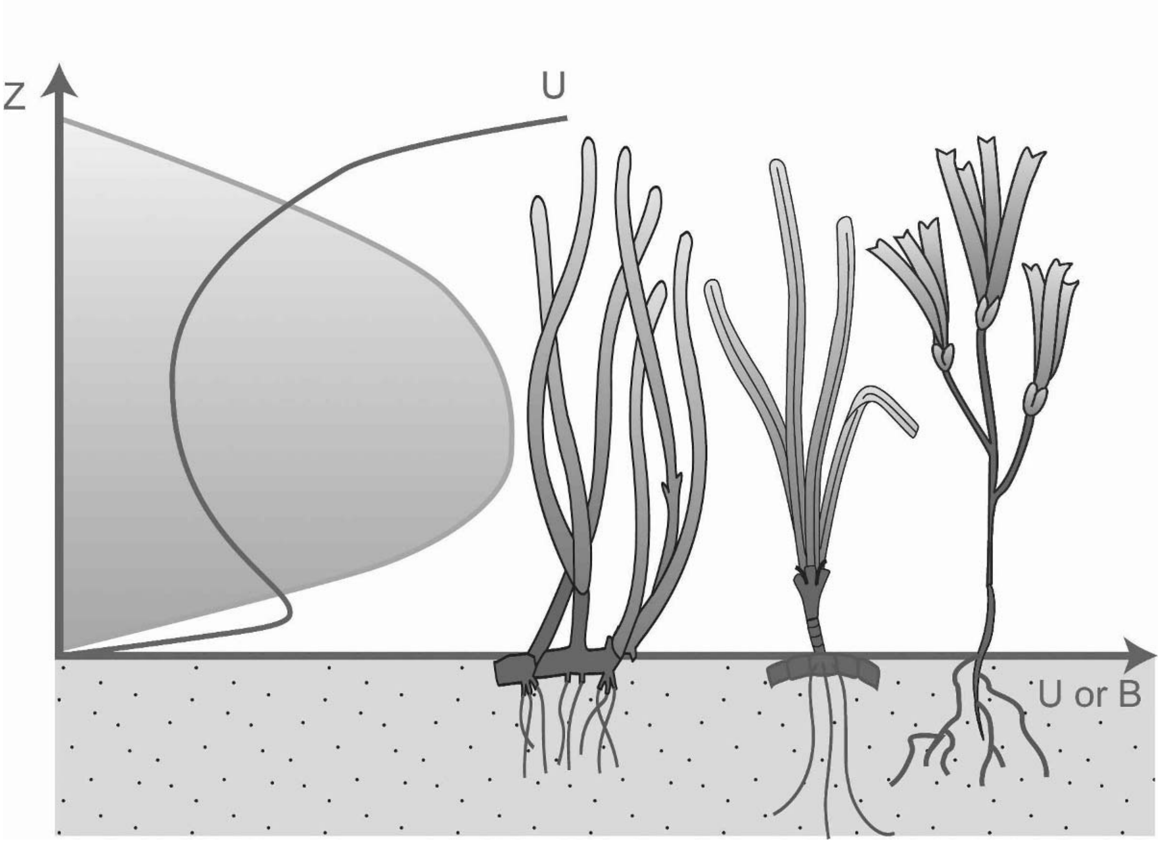

Fig. 6. Vertical velocity (*U*) profile (solid line) showing relative flow intensification near the bottom, which is a result of the vertical seagrass biomass (B) distribution (shaded area). *Z*, distance above the sediment interface. Adapted from Ackerman and Okubo (1993; *Zostera marina*). Also observed for *Thalassia testudinum* (koch, 1996), *Amphibolis griffithii* (van Keulen, 1997), and *Amphibolis antarctica* (Verduin and Backhaus, 2000).

due to the deflection of the current over the canopy and a loss of momentum within the canopy (Fonseca et al., 1982; Fonseca and Fisher, 1986; Gambi et al., 1990; Koch, 1996; Wallace and Cox, 1997; Koch and Gust, 1999; Verduin and Backhaus, 2000; Peterson et al., 2004). As a result, depending on the seagrass species and shoot density, water speed in the canopy can be 2 to >10 times slower than outside the bed (Ackerman, 1986; Gambi et al., 1990). This process can also trap water within dense seagrass canopies during low tide, leading to a water height difference between vegetated and adjacent unvegetated areas (Powell and Schaffner, 1991). Velocities within seagrass canopies are commonly <10 cm s^{-1} but can be as high as 100 cm s^{-1} (see review by Koch, 2001). Even relatively short seagrasses (*Zostera novazelandica*, 15 cm) or beds with relatively low densities (*Zostera marina*, 100–200 shoots m^{-2}) still seem to reduce velocity (Worcester, 1995; Heiss et al., 2000).

When measuring velocities at a relatively fine scale (cm), flow intensification near the bottom (i.e. relatively faster flows in the region of the sheaths or vertical stems, Fig. 6) may be observed depending on the vertical biomass distribution (Ackerman and Okubo, 1993; Koch, 1996; Koch and Gust, 1999; Nepf and Vivoni, 2000; Verduin and Backhaus, 2000; van Keulen and Borowitzka, 2002). This is due to the fact that the sheaths (e.g. *Thalassia testudinum* and *Zostera marina*) or stems (e.g. *Amphibolis griffithii* and *A. antarctica*) are less effective in reducing the flow and extracting momentum (Fig. 6) than the vegetated regions above the sheaths and stems that are filled with leaves. Similarly, velocities increase near the top of the canopy as the leaf area is reduced and eventually disappears.

A number of canopy flow models have been applied to terrestrial plant canopies using empirically-fit parameters to modify the law of the wall (review in Okubo et al., 2002). This approach has been recently

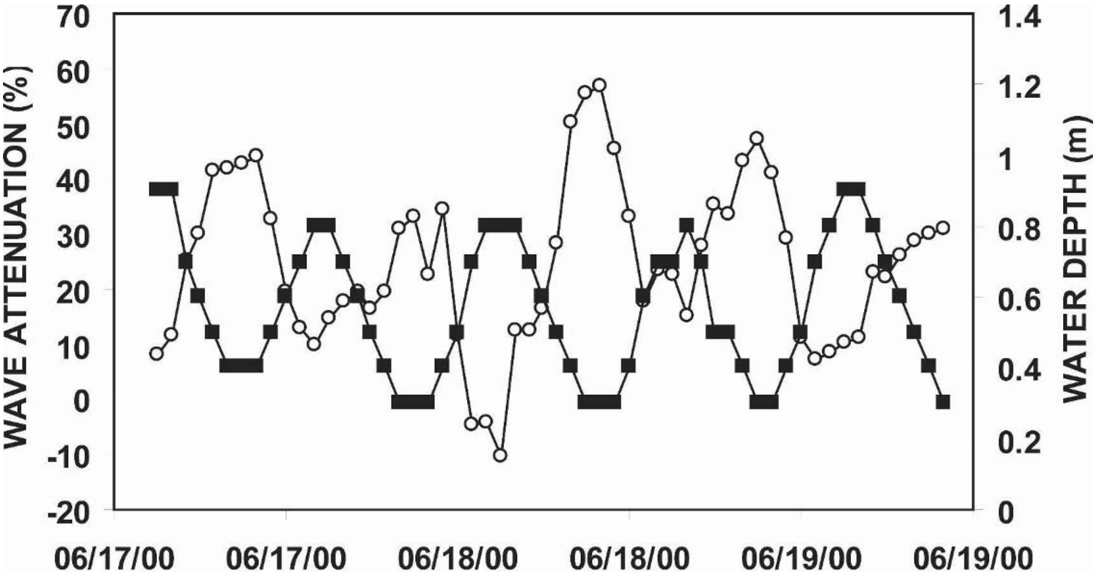

Fig. 7. Wave attenuation (open circles) as a function of water depth/tidal fluctuation (black boxes). Wave attenuation was based on the significant wave height in a *Ruppia maritima* bed in comparison to an adjacent unvegetated area at Bishop's Head Point, Chesapeake Bay, USA. Note that these data were collected in June when the plants were reproductive. Wave attenuation was highest at low tide when the canopy occupied the entire water column. Negative wave attenuation represents periods in which wave height was larger in the vegetated site than the unvegetated site. Source of data: E.W. Koch.

applied to *Z. marina* with some success, although there were a number of inconsistencies with field observations as would be expected (Abdelrham, 2003; Peterson et al., 2004). This type of approach provides some indication of the general pattern of flow within an eelgrass canopy, but its utility will likely be limited by species-specific differences in canopy vegetative profiles and the lack of detailed studies of canopy flow in these systems. Future development will need to apply the mixing layer analogy. Realistically, the ability to model canopy flow phenomena is a goal that speaks to the need for detailed canopy flow profiles in the laboratory and the field.

B. Wave Attenuation by Seagrass Canopies: A Concept in Development

"Seagrasses are able to modify current flow and sediment composition, yet little information exists describing their effect on waves." This statement with which Fonseca and Cahalan (1992) started their paper more than 10 years ago is still true today. Many papers begin by describing the importance of seagrasses, including their capacity to attenuate waves, but the studies which led to this generalization are few. A flume study measured wave attenuations between 20 and 76% over 1 m length when the plants were occupying the entire water depth (Fonseca and Cahalan, 1992), whereas field studies measured values between 1.6 and 80% (Koch, 1996; Prager and Halley, 1999). Our general understanding is that wave attenuation is highest when seagrasses occupy a large portion (>50%) of the water column (Ward et al., 1984; Fonseca and Cahalan, 1992; Fig. 7), but reduction in wave energy (15 s waves) has also been observed in a 5 m deep *Amphibolis antarctica* bed (Verduin and Backhaus, 2000) and reduction of orbital velocities (3–4 s waves) at a 15 m deep *Posidonia oceanica* bed (Granata et al., 2001) where the plants occupied only a small portion of the water column.

C. Monamis

Canopy flow is complex because it is a function of the drag or resistance exerted by the vegetation on the fluid, which is likely to vary spatially due to stem spacing and vertically due to the vegetation profile (Okubo et al., 2002). One important consequence of this realization is the propagation of wave-like oscillations or *monamis* (*mo* = aquatic plant; *nami* = wave; Ackerman and Okubo, 1993) caused by Kelvin-Helmholtz instabilities that generate large coherent vortices at the interface between the canopy and the overlaying water column, where the velocity profiles exhibit an inflection point. These vortices can penetrate into the canopy (Ghisalberti and Nepf, 2002) and interact with the flexible and buoyant plants in a hydroelastic response due to the buoyancy created by gas-filled lacunae and propagate downstream over the canopy causing the shoots to wave in a coherent manner (Ghisalberti and Nepf, 2002). This synchronous motion of seagrasses results in enhanced vertical transport between the water column and the canopy (Ghisalberti and Nepf, 2002). The ecological consequence of monamis is the potential to increase larval recruitment (Grizzle et al., 1996) and nutrient uptake.

D. Water Flow and Nutrient Uptake in Seagrass Canopies

Nutrient uptake at the canopy level is a function of water velocity. Increasing velocities lead to higher uptake of ammonium in *Thalassia testudinum* and *Halodule wrightii* (Thomas et al., 2000) and their epiphytes (Cornelisen and Thomas, 2002). At the same time, as velocity increases, the leaves bend, decreasing the obstruction/friction of the canopy. As a result, the efficiency of the canopy to remove ammonium from the water column decreases at high velocities (Thomas et al., 2000), unless leaf flapping due to monamis or the orbital motion of waves cause mixing within the canopy (Wallace and Cox, 1997; Koch and Gust, 1999; Ghisalberti and Nepf, 2002).

The depth that the upper, highly turbulent flow at the top of the canopy (with relatively high nutrient levels) penetrates into the canopy is a function of the percent of the water column that is occupied by the canopy and the density of the shoots (Nepf and Vivoni, 2000). Dense canopies occupying most of the water column have narrow zones of high turbulence “skimming flow” at the top of their canopies. Therefore, the flux of nutrients to areas deep within the canopy may be limited.

Mixing and vertical exchange between the water column and the seagrass canopy are a function of the prevailing hydrodynamic conditions and also of how seagrasses respond to them by bending, flexing, waving, etc. When leaves bend under strong currents, the canopy height decreases collapsing the leaves onto each other, “closing” the canopy (Fig. 8A and B) and limiting vertical exchange (Koch and Gust, 1999). In contrast, when seagrasses are exposed to monamis in unidirectional flows, or wave-dominated conditions, the back and forth motion of the leaves (Fig. 8C, D, and E) enhances vertical exchange (Koch and Gust, 1999; Ghisalberti and Nepf, 2002). This suggests that nutrient uptake should be highest at the upper portion of the canopy (Nepf and Vivoni, 2000), but this is also where the oldest and least biologically active portions of the seagrass leaves are located. Perhaps the vertical mixing zone at the top of the canopy is more important in the recruitment process bringing larvae and spores into the canopy (Grizzle et al., 1996) than in the flux of nutrient and carbon molecules.

E. Faunal Recruitment in Seagrass Canopies

The ecological role of seagrass canopies in the ecology of benthic and pelagic organisms is becoming increasingly clear, especially in the case of crustaceans and fish (e.g. Kenyon et al., 1999; Thayer et al., 1999; Etherington and Eggleston, 2000; Nagelkerken et al., 2001). Many of these organisms are ecologically and economically important species that settle in or on the leaves and shoots of seagrasses as epiphytes for a portion of their life history (Eckman, 1987; Borowitzka and Lethbridge, 1989; Newell et al., 1991; Grizzle et al., 1996). Larval settlement appears to be a function of larval supply (i.e. flux), the fluid dynamic interaction with boundaries on which settlement occurs, and larval behavior (e.g. Abelson and Denny, 1997; Okubo et al., 2002). As indicated above, flows through vegetated areas are quite complex, and consequently, a mechanistic understanding of faunal recruitment in seagrass canopies is lacking at present, although recent efforts have been directed to these ends (e.g. Palmer et al., 2004). Fortunately, there are a number of processes and taxonomic systems including sediment dynamics in which the role of canopy flow has been examined.

A recent estimate from the field indicates that the potential for particle contact with a leaf surface approaches certainty under particular flow conditions in a *Zostera marina* canopy (Ackerman, 2002; see Section IV.D). The situation is more complex in terms of larval settlement. The general pattern that emerges is that settlement is higher in vegetated areas in the case of bivalve larvae (e.g. scallops) settling on *Z. marina* leaves (Eckman, 1987) and filamentous benthic algae (Harvey et al., 1995). For example, blue mussel recruitment on *Z. marina* leaves can

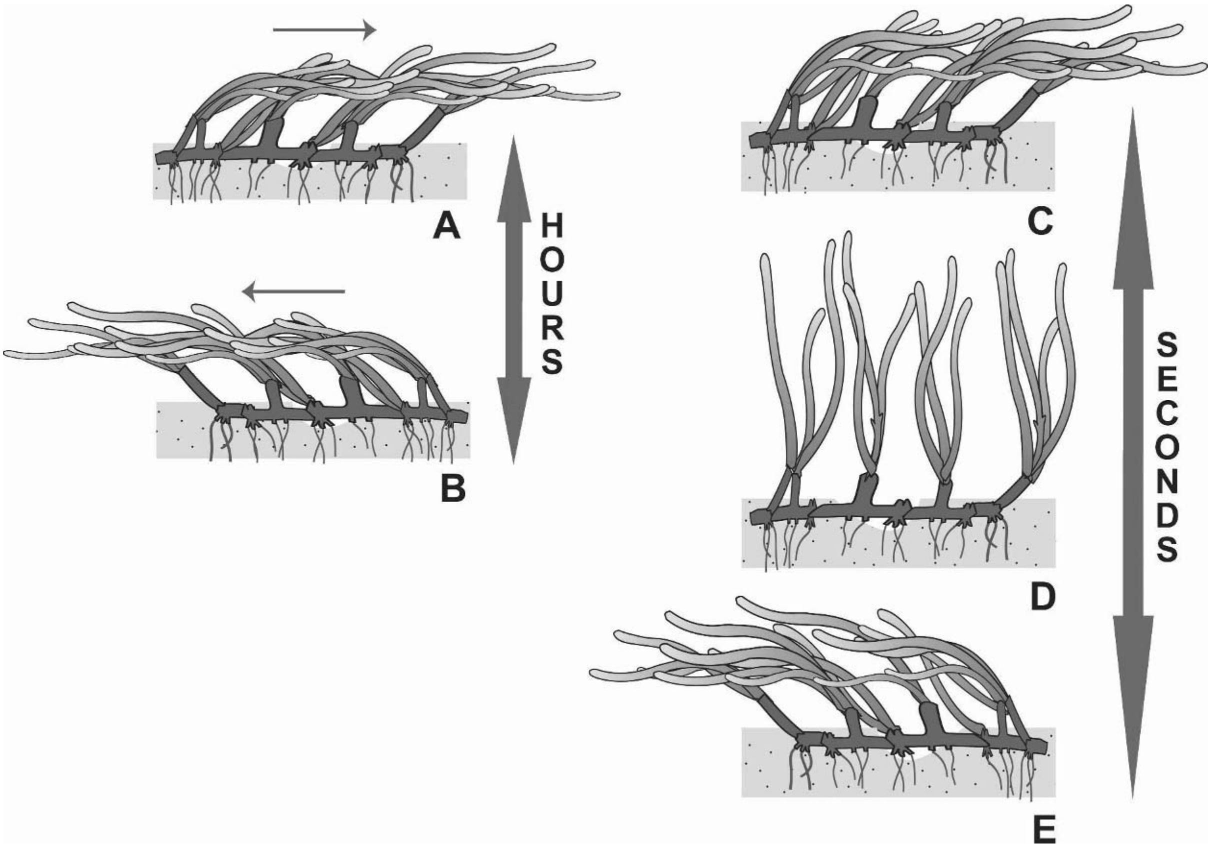

Fig. 8. Bending cycles seagrass canopies undergo when exposed to unidirectional (A and B) and oscillatory (C, D and E) flows. During a flood tide, leaves bend in the direction of the flow (A) and hours later, during the ebb tide, leaves bend in the opposite direction (B). These are considered "closed" canopies where conditions within the canopy are relatively stagnant. In contrast, in wave-dominated habitats, seagrass leaves bend in one direction (C), become somewhat upright (D) and bend in the opposite direction (E) in a matter of seconds (wave period). This process leads to rapid "opening" (vertical leaves) and "closing" (bent leaves) of the canopy and enhances the exchange between the canopy and the water column above it (Koch and Gust, 1999). The intermediate phase (D) is non-existent in habitats characterized by swell—leaves just sway back and forth, never becoming upright or fully extended (see Fig. 3A).

be considerable (i.e. >90 postlarvae per cm of leaf; Newell et al., 1991; reviewed in Ackerman et al., 1994), and it has been suggested that the monamis facilitate high settlement rates through increasing the likelihood of larval encounter with undulating leaves and the mixing that occurs under monami conditions (Grizzle et al., 1996). Clearly, plant–animal interactions mediated by the interaction of seagrass canopies and fluid dynamics is an important subject where future inquiry is warranted.

F. Direct and Indirect Effects of Tides on Seagrass Canopies

Seagrasses exist in areas that are affected by tidal flow, which can lead to desiccation of leaves, and limit the depth distribution and light availability of habitats. Tides can also intensify or relieve the effect of waves on seagrass canopies. As indicated in Section II, most of a wave's energy (orbital velocity) is located near the water surface. Therefore, assuming an equal wave climate, seagrass canopies are exposed to more wave energy during low tides than at high tides (e.g. Ochieng and Erftemeijer, 1999; Koch, 2001; Krause-Jensen et al., 2003; Middelboe et al., 2003). The degree of tidal exposure and the capacity of different seagrass species to tolerate desiccation and high light levels (including ultraviolet-B radiation) affect their minimum depth of distribution (Stapel et al., 1997; Koch, 2001). Additionally, tides also affect the light availability in seagrass habitats. During periods of high or low tide at noon, seagrasses are exposed to extreme light levels in the middle of the day and intermediate light levels in the morning and afternoon (ebb or flood), i.e. these plants will be exposed to long hours of saturating light. In contrast, when high tides occur in the morning and afternoon (semi-diurnal tides), the light levels in the middle of the day may be saturating (ebb or flood), but the number of hours of saturating light will be reduced due to the high water during the remainder of the day (Koch and Beer, 1996). These scenarios are also complicated by turbidity (Koch and Beer, 1996).

G. Self-Shading in Seagrass Canopies Exposed to Tides, Currents and Waves

Although seagrass leaves contain gas-filled lacunae and tend to become erect in the water column, the leaves will comply with the flow generated by tidal currents and waves. During low tide, when seagrass leaves in the intertidal area rest on top of each other, self-shading is at its maximum. This process is reversed as the tide returns to its full level. Under unidirectional flows, the degree of bending in the direction of the flow is a function of the magnitude of the current (Fonseca et al., 1982). It follows that self-shading is expected to be highest when currents are strongest and the leaves are collapsed onto each other. Leaf flapping also occurs under wave-dominated conditions (Koch and Gust, 1999), relieving some of the self-shading as flecks of light penetrate the leaf mass or canopy at the frequency of flapping.

Short-term (seconds) flecks of light referred to as "lightflecks" (Fig. 9), are also generated in areas exposed to waves. The light that reaches the water surface is focused at the crest of the waves and dispersed at the trough of the waves (Wing and Patterson, 1993; Fig. 9). This results in "dancing lights" in shallow areas such as seagrass beds due to the propagation of lightflecks. The frequency of lightflecks resembles that of the passing waves (Wing and Patterson, 1993). Although the effect of lightflecks on seagrass productivity was never tested, productivity is likely to be enhanced as has been demonstrated in phytoplankton and macroalgae (Dromgoole, 1988; Greene and Gerard, 1990; Wing and Patterson, 1993; Wing et al., 1993).

H. Seagrass Canopies as Depositional Environments: Not a Universal Concept

Historical evidence of seagrass beds as depositional environments is borne out of the loss of seagrasses (due to wasting disease or grazing) resulting in the erosion of sediments (Rasmussen, 1977; Hine et al., 1987). Many authors suggested that seagrass canopies are areas where sediments deposit and accumulate (Grady, 1981; Almasi et al., 1987; Patterson and Black, 1999; Gacia and Duarte, 2001), largely due to the reduction of velocity and turbulence intensity (e.g. Fonseca et al., 1983; Ackerman and Okubo, 1993; Worcester, 1995; Verduin and Backhaus, 2000; Granata et al., 2001), i.e. a reduction in stress on the sediment surface due to reduced flow speed within the canopy that leads to a reduction in resuspension and thus, an increase in accumulation (Lopez and Garcia, 1998). This accumulation can be seasonal, especially during summer when seagrasses are at their maximum density, but in winter, when the plants disappear or decrease in density, resuspension may be greater than deposition (van Keulen and Borowitzka, 2003). Often, the presence of seagrass rhizomes and roots in the sediment through the winter is sufficient to stabilize the sediments. The size of the seagrass species also affects sediment accumulation. Although bigger species may be better for sediment deposition (Fonseca and Fisher, 1986), small seagrasses such as *Halophila decipiens* and *Zostera novazelandica* can still alter the sediments they colonize (Fonseca, 1985, 1989; Heiss et al., 2000).

More recent efforts have focused on the role of seagrass canopies in trapping and retaining sediments, which appears to be related to sediment contact with leaves (Gacia et al., 1999; Agawin and Duarte, 2002). Epiphytic layers on seagrass leaves may contribute to the entrapment of particles in seagrass beds by increasing the roughness of the canopy and increasing the boundary layer on the leaf surface; i.e. expanding the area in which water flow is reduced thereby facilitating the entrapment of particles (Vermaat et al., 2000). Whereas, seagrasses are generally viewed as agents that trap particles and stabilize the sediments, resuspension, especially of fine sediments with high organic content, can occur under high wave exposure and current flow (Fonseca et al., 1983; Fonseca and Bell, 1998). In highly wave-exposed sites where seagrasses do not attenuate

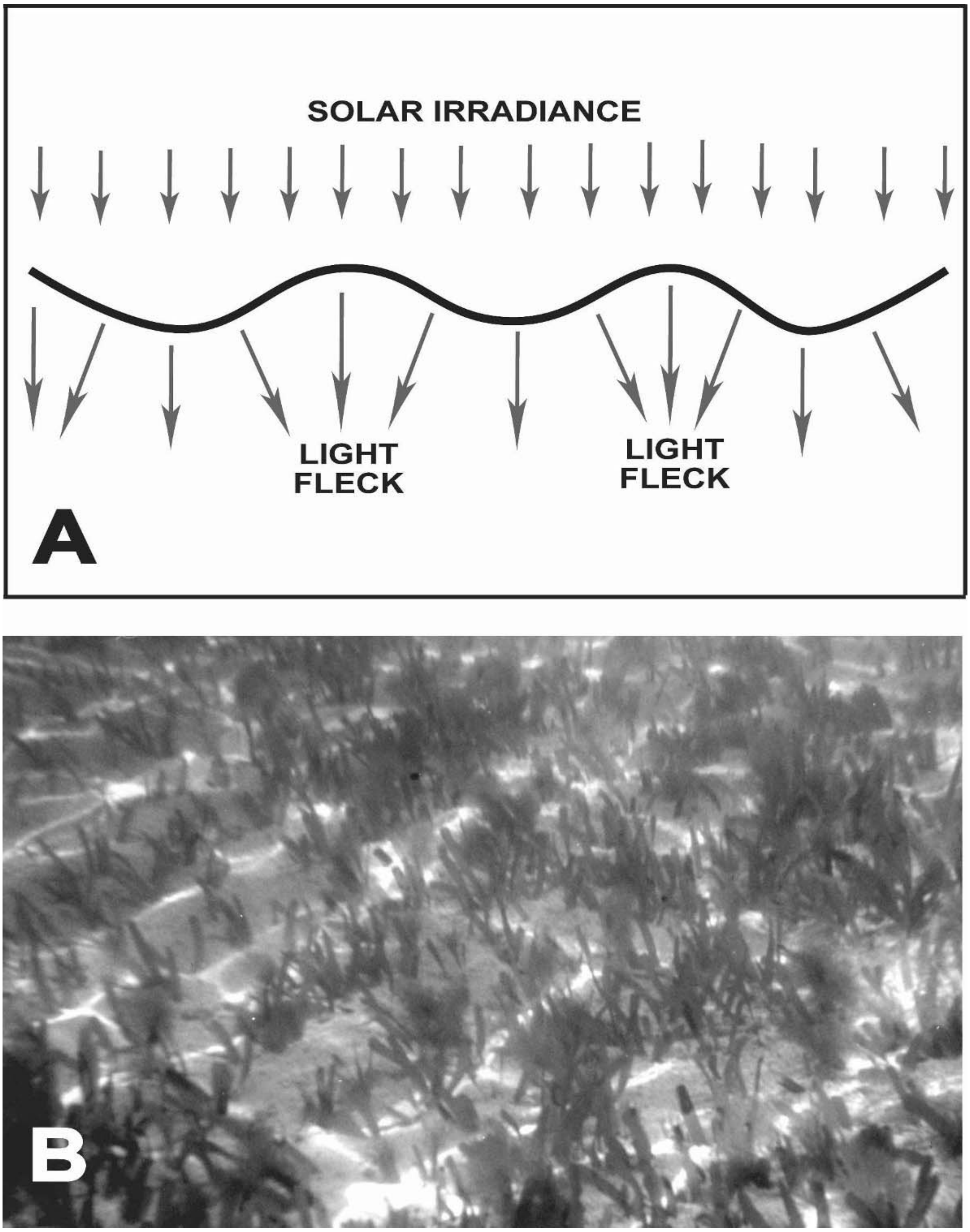

Fig. 9. Lightflecks form in areas where the surface of the water is not flat, instead, it has waves (A). The light that reaches the water surface (vertical arrows above wave) is focused by wave crests and is dissipated by wave troughs. In the area where the light is focused, lightflecks form. Under the right combination of water depth and wavelength (i.e. water depth in the focusing range), lightflecks can be observed on the seafloor as seen in a shallow *Thalassia testudinum* bed in the Florida Keys, USA (B). Photo: E.W. Koch.

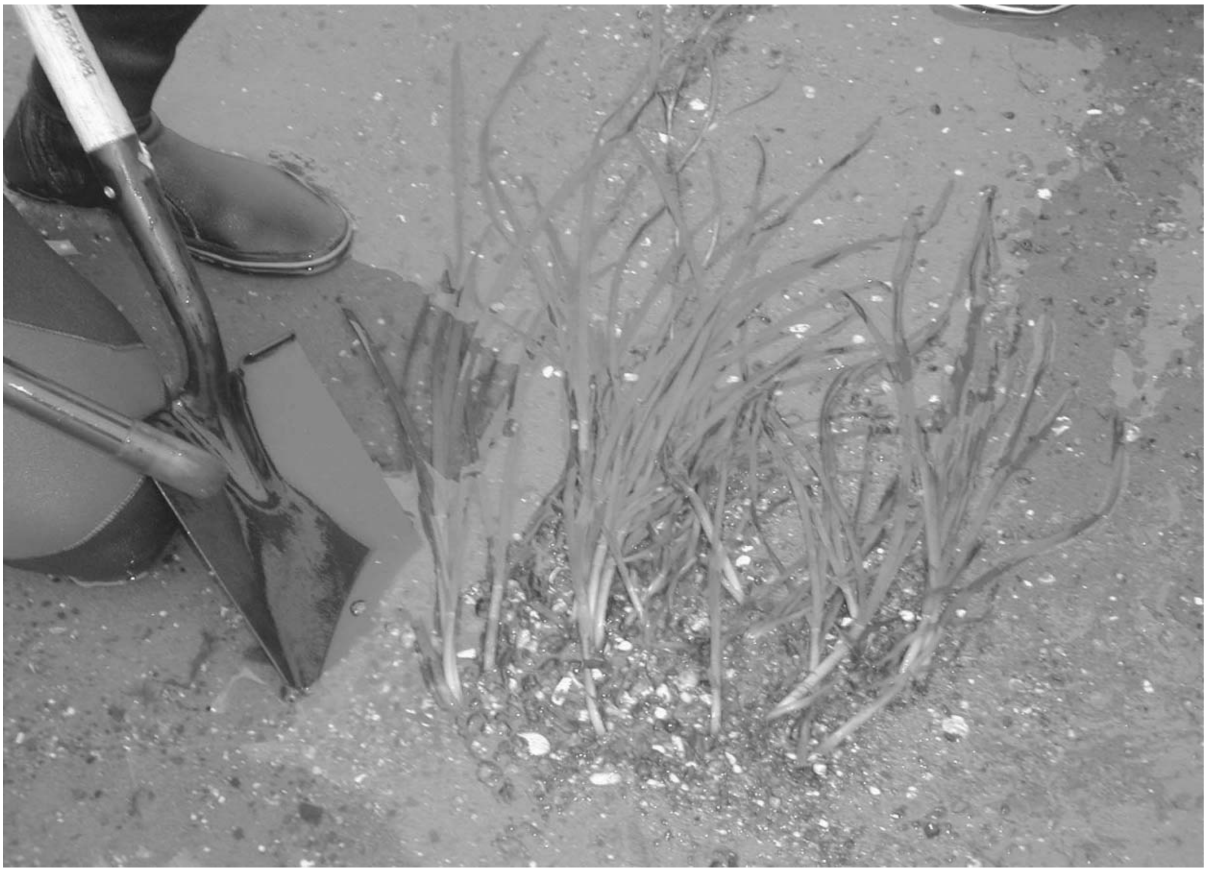

Fig. 10. Patch of *Zostera marina* at Crown Breach, Alameda, California, USA, containing coarser sediment than the surrounding area. This may be a result of turbulence generated by the seagrass leaves (Koch, 1993). As a result, finer particles are resuspended while coarser particles remain. Note that this patch was located at a water depth of 0.9 m and is a single genet (i.e. a true clonal unit) as it originated from one single seed that germinated in February 2003. Photo taken in August 2003 by Mark Fonseca.

water flow as effectively as in unidirectional (tidal) flows (Koch and Gust, 1999), sediment characteristics within and outside seagrass beds differed little to none (Hoskin, 1983; Edgar and Shaw, 1991; Koch, 1999b; van Keulen and Borowitzka, 2003). Actually, in some cases, sediment in a vegetated area can be coarser than in the adjacent unvegetated area (Koch, 1993; Fig. 10).

VI. Hydrodynamically-Mediated Processes at the Landscape Level (100–1000 m)

A number of studies have analyzed how seagrass canopies alter local hydrodynamic conditions and, with that, affect their own productivity, associated biota, sediments, and the water column surrounding them. In contrast, hydrodynamic studies in seagrass habitats at the landscape level are less common. While most studies at the canopy level assume that the shoot density is homogenous (Vidono et al., 1997), at the landscape level, it is becoming clear that seagrasses are spatially heterogeneous (Robbins and Bell, 1994). In this section, we address flow-related causes of seagrass heterogeneity and hydrodynamic consequences of seagrass patchiness.

A. Seagrass Landscapes and the Substrates they Colonize

Although seagrass landscapes represent a simpler system than terrestrial landscapes in terms of species diversity and structure (Robbins and Bell, 1994), a mosaic of different seagrass species, shoot characteristics, associated biota, and sediment elevations and types exist. Responses of individual plants to water

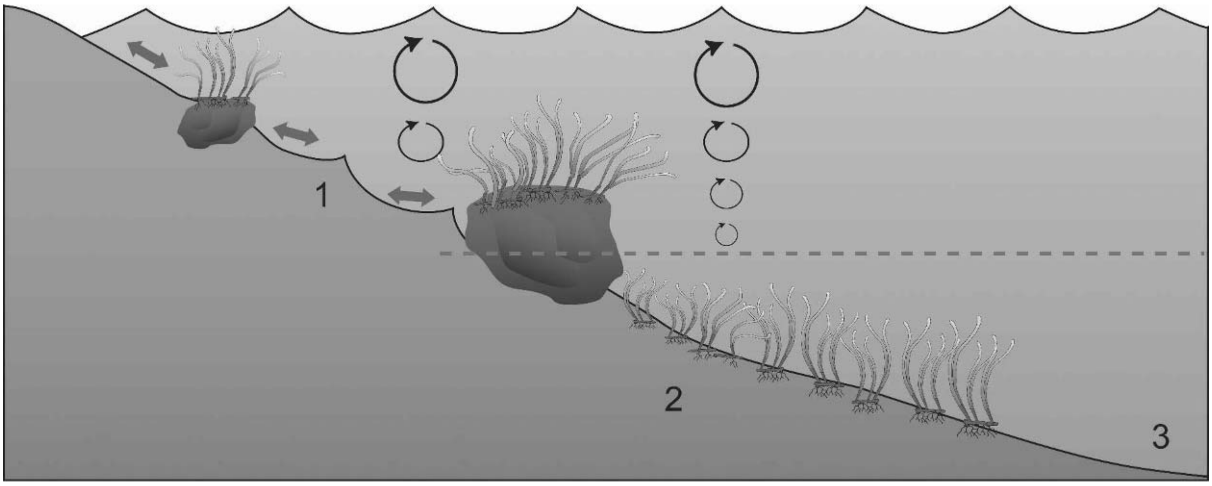

Fig. 11. Diagram of seagrass distribution in habitats characterized by high wave energy. In shallows areas where waves are felt on the bottom (1), sediment movement is constant (arrows) not allowing seagrasses to become established. In this area (1), some seagrasses are capable of colonizing non-shifting substrates such as rocks. In contrast, in deeper areas sheltered from the waves (2, i.e. below the maximum wave penetration depth represented by the dashed line), sediment movement is reduced allowing seagrasses to become established. The maximum depth of distribution of the seagrasses is limited by light availability (3).

motion accumulate and may be the basis of seagrass landscape patterns perceived at coarser scales of resolution (Fonseca, 1996). Hydrodynamic forces may also affect seagrass habitat requirements such as light availability, sediment characteristics, and substrate stability (Ben Alaya, 1972; Cooper, 1982; van Katwijk and Hermus, 2000; Fig. 10), thereby altering the pattern of distribution even further (feedback).

In shallow areas with relatively high wave energy, the substrate is usually characterized by coarse shifting sand (Dan et al., 1998) and/or rocks. The shifting sediments remain unvegetated due to continuous erosion and burial of recruits (Shepherd and Robertson, 1989; Hemminga and Duarte, 2000; Frederiksen et al., 2004). Some seagrasses are able to colonize rocks (a stable substrate) in these shallow, high wave-energy areas by modifying their root system. The genus *Phyllospadix*, which colonizes the rocky intertidal in the north Pacific (Wyllie-Echeverria and Ackerman, 2003), is an example of this. However, in Corsica (Mediterranean), *Posidonia oceanica* is found on rocks in shallow areas where sand grains are moving back and forth every few seconds due to the passage of waves (Fig. 11) (Koch, personal observation), yet it colonizes soft substrates at depths below the maximum wave penetration depth. Other seagrasses capable of colonizing hard as well as soft substrates are *Thalassodendron ciliatum* (Bandeira and Nilsson, 2001) in Mozambique (Bandeira, 2002) and *Amphibolis antarctica* in Australia (Ducker et al., 1977). What makes one species more adaptable to different substrates than others is presently unknown. Landscape level studies for seagrasses on rocky substrates are limited; therefore, the remaining discussion will address seagrass meadows colonizing soft substrates.

B. Hydrodynamically Generated Patchiness in Seagrass Meadows

The mosaic of patterns observed in seagrass landscapes is often a result of natural perturbations such as erosion and burial by sand waves (Harlin and Thorne-Miller, 1982; Fonseca et al., 1983; Marbà et al., 1994; Marbà and Duarte, 1995; Fonseca and Bell, 1998; Bell et al., 1999; Fig. 12) and/or disturbances caused by fauna (Orth, 1975; Ogden, 1980; Preen, 1995), storms (Preen et al., 1995; Fonseca and Bell, 1998) and/or disease (den Hartog, 1987). Anthropogenic causes (eutrophication, boat and mooring scars, fishing gear scars) can also contribute to seagrass patchiness (Cambridge, 1975; Walker et al., 1989; Creed and Filho, 1999; Orth et al., 2002). Here we will focus on flow-related generation of patchiness.

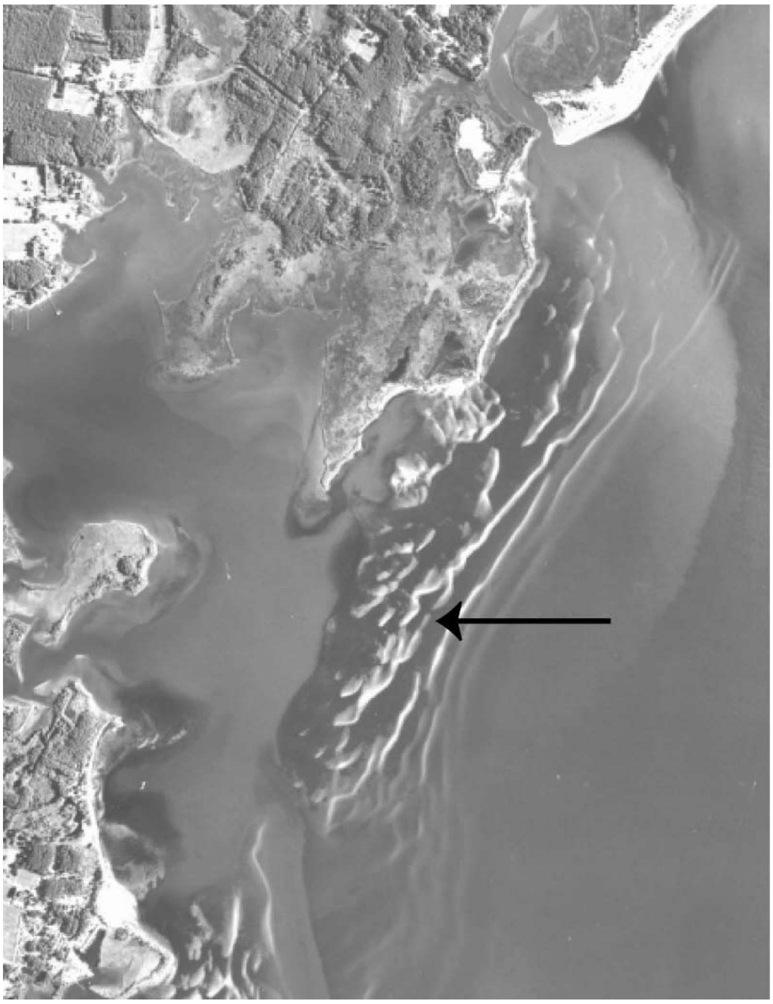

Fig. 12. Complex seagrass landscape due to the presence of sand waves (arrow) in a *Zostera marina* bed at Horn Harbor, Chesapeake Bay, USA. Photo: R.J. Orth.

The disturbances that lead to patchiness in seagrass landscapes range in scale from the complete but local destruction of seagrass ecosystems (Dan et al., 1998) to the creation of smaller (10's of meters) unvegetated depressions in continuous meadows, termed "blowouts" (Patriquin, 1975; see review in Short and Wyllie-Echeverria, 1996; Fonseca and Bell, 1998). The magnitude and frequency of disturbances is what determines the degree of patchiness of a seagrass meadow (Fonseca et al., 1983; Fonseca and Bell, 1998; Hemminga and Duarte, 2000). It can therefore be assumed that more extreme events would result in erosion and complete or partial loss of seagrasses (with little recovery), whereas periods of reduced disturbance may result in coalescence of the patches and the formation of more continuous meadows (Fonseca et al., 1983; Kirkman and Kirkman, 2000). This concurs with numerous reports of widespread loss of meadows as a result of hurricanes and cyclones (Birch and Birch, 1984; Williams, 1988; Rodriguez et al., 1994; Preen et al., 1995; Moncreiff et al., 1999; Whitfield et al., 2002), and the extensive colonization of seagrasses (pioneering or climax species) during periods of reduced disturbance (Kirkman, 1985; Kendrick et al., 2000). Note that some studies report no damage to seagrasses after the passage of hurricanes (Thomas et al., 1961; Tilmant et al., 1994; Dawes et al., 1995).

In areas with continuous high wave energy, seagrass ecosystems can be: (i) non-existent (Dan et al., 1998); (ii) depth restricted (when sufficient light is available, seagrasses colonize areas below the maximum wave penetration depth; Krause-Jensen et al., 2003; Middelboe et al., 2003); (iii) dominated by more robust species (e.g. *Amphibolis griffithii* and *Posidonia coriacea*); and (iv) patchier as the disturbance of high waves may hinder the lateral expansion of some seagrass beds (Kendrick et al., 2000; Frederiksen et al., 2004). In contrast, in sheltered waters, seagrass meadows tend to be more continuous and are colonized by relatively more fragile species (e.g. some *Posidonia* spp) (Kirkman and Kuo, 1990). Under calm conditions, creation of openings in meadows appears not to lead to further wide-scale loss, although regrowth into the damaged areas can be slow (Walker et al., 1989; Meehan and West, 2000; Orth et al., 2002). The degree of wave exposure can be quantified by applying the relative wave exposure index (REI) first developed by Keddy. This index takes into account the wind direction and intensity and fetch and has been successfully linked to landscape features in seagrass habitats (Fonseca and Bell, 1998; Fonseca et al., 2000, 2002; Hovel et al., 2002; Krause-Jensen et al., 2003; Frederiksen et al., 2004). When wave-dissipating structures (e.g. sand bars, sills, coral or oyster reefs) occur in the seagrass system, the bathymetry may also have to be taken into account in order to properly estimate the wave exposure using the REI.

A mixture of unvegetated and densely vegetated areas in close proximity may characterize intermediate disturbance regimes. For example, *Posidonia sinuosa* meadows in habitats of moderate water flow are characterized by dense rows of plants interchanged with strips of bare sand (Bridgwood, 2002). A similar gradient of patterns has been reported for meadows of *Zostera marina* subject to gradients in velocity and wave energy (Fig. 12), with the proposal that the structural integrity of the habitat would deteriorate with increasing habitat fragmentation (den Hartog, 1971; Fonseca et al., 1983; Fonseca and Bell, 1998).

Another common cause for complex seagrass mosaic patterns is the hydrodynamically-mediated movement of sand waves and sand dunes through seagrass meadows (Marbà et al., 1994; Walker et al., 1996; Bridgwood, 2002; Paling et al., 2003; van Keulen and Borowitzka, 2003; Frederiksen et al., 2004). Changes in sediment height, a result of water flow, can be significant and rapid (10's of cm over periods of hours) (Paling et al., 2003), and larger sand dunes can travel through meadows on a time scale of months (Walker et al., 1996; Bridgwood, 2002; van Keulen and Borowitzka, 2003). The degree to which these large amounts of sediment negatively affect the seagrasses creating unvegetated patches depends on their tolerance for sedimentation, the amount of sediment deposited, and the period the plants remain buried. Sedimentation rates of 2 to 13 cm year^{-1} can be coped with by large (e.g. *Enhalus acoroides*) as well as by fast growing (e.g. *Halophila*) seagrasses as well as by plants with vertical stem elongation (e.g. *Cymodocea nodosa*, *C. serrulata* and *Syringodium isoetifolium*) (Vermaat et al., 1996). Subaqueous dune migration appears to maintain *Cymodocea* meadows in a continuous state of colonization which is ultimately responsible for the characteristic patchy landscape (Marbà and Duarte, 1995). Even when sediments completely cover the leaves of small, slow-growing plants, some seagrasses are able to survive as long as the sediment is removed by currents or waves in a matter of weeks (*Halodule wrightii* survived after being buried for 2 months; Phillips, 1980). Other seagrasses such as *Posidonia oceanica* are able to increase vertical growth from 5 to 7 mm year^{-1} to 52 mm year^{-1} when (partially) covered by sand waves (Boudouresque and de Grissac, 1983). In contrast, *Zostera marina* seems to have little or no tolerance to sedimentation regardless of the sediment type (Mills and Fonseca, 2003).

C. Effect of Patchiness on Flow and Flow-Related Processes

When considering processes in seagrass meadows, spatial homogeneity is usually assumed, but in nature, patchy seagrass landscapes are more common than homogenous ones. This patchiness may have a major effect on physical, geological, chemical, and biological processes. For example, gaps in the canopy allow an accelerated influx of water into the canopy (Granata et al., 2001), replenishing nutrients, introducing spores and propagules, eroding sediment and increasing mixing in general. The distance currents can penetrate the edge of a seagrass bed before becoming equilibrated with respect to momentum has been estimated to be between 1 m (Fonseca and Fisher, 1986) and 50 boundary layers (assumed to be equal to the height of the canopy; Nowell and Jumars, 1984; Granata et al., 2001).

These values can be affected by the density of the bed and the vertical distribution of biomass. In dense beds, unidirectional water flow is smoothly directed over the top of the seagrass canopy as "skimming flow" (Nowell and Jumars, 1984; Fonseca and Kenworthy, 1987), effectively trapping a layer of water within the canopy (Koch and Gust, 1999), i.e. increasing the residence time. Under such conditions, nutrient concentrations within the vegetation may be quite low (Moore et al., 1996). In contrast, a reduction in shoot density leads to increased flow intrusion and velocity within the canopy (van Keulen, 1997). Therefore, reducing seagrass density could permit an increase in turbulence and mixing within the meadow, with an associated increase in nutrient exchange and uptake, and the potential for increased sediment resuspension. This subject needs further attention.

VII. Hydrodynamic Processes at the Meso-Scale Level (>1,000 m)

A. Seagrasses in the Biosphere

Seagrass meadows are one of several plant communities found in coastal areas around the world. Marshes and mangroves line the intertidal area of shorelines of seagrass-colonized temperate and tropical systems, respectively. The hydrodynamic functions of each of these communities can be quite similar: attenuation of currents and waves leading to deposition of particles and the stabilization of the substrate (Knutson et al., 1982; Knutson, 1988; Massel et al., 1999; Möller et al., 1999). When considering these communities as a part of a larger coastal ecosystem, interactions between seagrasses and marshes/mangroves as well as with adjacent animal communities such as oyster and coral reefs start to emerge (see Section VII.B).

Water masses may have traveled over extensive distances, interacting with pelagic and benthic organisms before they reach seagrass beds. For example, during the flood tide, water masses may travel over sediments colonized by a variety of microalgae and benthic organisms such as a coral polyps and reefs before reaching the seagrass bed. In contrast, during ebb flow, the water that reaches seagrass beds may have resided in an estuary, a mangrove, or a marsh system for a period of time. Each of these plant and animal communities tends to alter the water mass in its chemical and/or physical properties directly or indirectly (Bulthuis et al., 1984). When these waters are then transported into seagrasses meadows, they also affect these plant communities. Therefore, a link between seagrasses and adjacent plant and animal communities is expected.

B. Linking Seagrasses and Adjacent Communities via Water Flow

1. Linking Seagrasses and Adjacent Systems via Tidal Fluxes

Tidal flows link terrestrial, estuarine, and marine systems. The residence time of a water mass in a seagrass habitat (determined by the tidal fluxes) may have a profound effect on seagrass distribution. Short residence times (days) allow pollutants and excess nutrients to be flushed out of a system before harming seagrasses (Kitheka et al., 1996). In contrast, long residence times promote the accumulation of nutrients and the growth of phytoplankton and nuisance algae while suppressing the growth of seagrasses via low light availability (Rysgaard et al., 1996; Herbert, 1999).

Coral reefs, seagrass beds, and mangrove forests often co-occur in tropical coastal systems suggesting an interaction of sorts, determined by tidal flows. For example, coastal wetlands such as marshes and mangroves assimilate nutrients leaching from land and thereby reduce the nutrient level reaching adjacent seagrass systems (Valiela and Cole, 2002) during ebb flows. These authors suggested that land-derived N loads from 20 to 1,000 kg N ha^{-1} year^{-1} seem to be a critical range for seagrass survival in shallow waters. When N loads are higher, wetlands are no longer able to remove sufficient N through denitrification, and N burial, and tidal currents will carry the excess nutrients into the seagrass beds. Excess nutrients can then lead to the loss of the seagrasses. Therefore, adjoining plant systems (wetlands and seagrasses) are not isolated units but are likely to be linked (Valiela and Cole, 2002).

Seagrass beds are among the most productive systems on the planet (Dring, 1994) and experience relatively low grazing losses with most leaf production being shed (Cebrian and Duarte, 2001; Mateo et al., Chapter 7). This amounts to a considerable quantity of detrital material which can remain within the seagrass meadow or can be exported. The fate of seagrass detritus depends, to a large extent, on the magnitude of currents, waves, and tides (Ochieng and Erftemeijer, 1999) and the nature of the leaves: some leaves float on becoming detached while others sink (Zieman et al., 1979). Floating leaves are more likely to be exported by tidal currents, but leaves that sink and form detritus locally may also be exported onto adjacent beaches or the deep sea during storm events and/or spring tides (Hemminga and Nieuwenhuize, 1990; Kirkman and Kendrick, 1997; Ochieng and Erftemeijer, 1999). It appears that in many instances detritus remains within the originating ecosystem, being recycled more or less *in situ* (Hemminga and Nieuwenhuize, 1991; Paling, 1991). In other cases, large amounts of seagrass detritus are transported into adjacent estuaries contributing to the estuarine carbon cycle (Bach et al., 1986; Cebrian and Duarte, 2001; Mateo et al., Chapter 7). Seagrass fragments have even been found at great depths in ocean basins ($>1{,}000$ m) where, it is postulated, they comprise an important food source for a number of invertebrate detritivores (Menzies et al., 1967; Menzies and Rowe, 1969; Wolff, 1976, 1979; Suchanek et al., 1985), as well as pelagic fishes and crustaceans (Williams et al., 1987). Litter washed up onto beaches also supports a wide range of invertebrates (Kirkman and Kendrick, 1997; Ochieng and Erftemeijer, 1999), and the location where the litter is deposited (high tide line or storm line) determines where invertebrates will find the highest availability of food. Litter that remains in shallow waters provides protection from erosion (Ochieng and Erftemeijer, 1999) and a habitat for juvenile fish (Lenanton et al., 1982; Robertson and Lennaton, 1984), but the reliability of this habitat depends on the local hydrodynamic conditions.

Tidal flows do not only link adjacent communities but can also isolate them. For example, in an estuary in Kenya, organic particles efflux and reflux between mangroves and seagrasses during each tidal cycle (Hemminga et al., 1994). During the ebb, POM effluxes from the mangroves reaching the seagrasses; during the flood, particles resuspended in the seagrass meadow (in part, particles generated in the mangroves and deposited in the seagrasses) reach the mangroves (Hemminga et al., 1994). These particles never make it to the adjacent coral reef due to trapping of the high turbidity plume by the tide and onshore winds (Fig. 13; Kitheka, 1996; Kitheka et al., 1996; Miyajima et al., 1998). Turbid waters could be detrimental to the reef-forming coral polyps (Johannes, 1975). As a result of the wave attenuation by the coral reef and the tidal isolation of the corals, mangroves, seagrasses and the coral reef can co-exist just a few kilometers apart along the Kenyan coast. This process is likely to also apply to other reef–seagrass–mangrove associations throughout the world.

2. Linking Seagrasses and Adjacent Ecosystems via Wave Attenuation

Several plant and animal communities (mangroves, marshes, corals, and oyster reefs) adjacent to seagrass meadows tend to attenuate waves, protecting shorelines from erosion (Knutson et al., 1982; Knutson, 1988; Massel et al., 1999; Möller et al., 1999). The decrease in waves by mangroves and marshes leads to sediment deposition (Othman, 1994) and, consequently, reduced water turbidity. A mangrove forest as narrow as 50–150 m can completely attenuate wave heights of up to 1 m (Othman, 1994), while a marsh can attenuate more than 80% of the incoming wave energy (Möller et al., 1999). Theoretically, seagrasses could benefit from this wave reduction especially during ebb flows as the water mass that resides in the mangroves or marshes will have lower turbidity. In turn, sub-tidal seagrass meadows adjacent to mangroves and marshes can minimize the impact of waves on marshes and mangroves via wave attenuation (van Katwijk, 2000).

Seagrasses also require relatively sheltered conditions in order to become established and thrive (Fonseca and Bell, 1998; Robbins and Bell, 2000; Koch, 2001), conditions that may have been previously found in the shelter of the once extensive oyster reefs in Chesapeake Bay (USA) and of sand bars in Tampa Bay (USA) (Lewis, 2002). Whereas some wave attenuation is expected to be beneficial for seagrass establishment, excessive wave attenuation may also be detrimental to seagrasses. When wave energy is extremely low, sediments tend to be relatively fine and to have elevated organic content (Wanless, 1981; Almasi et al., 1987; Fonseca, 1996; Fonseca and Bell, 1998), conditions which are not always favorable to seagrasses (Koch, 2001).

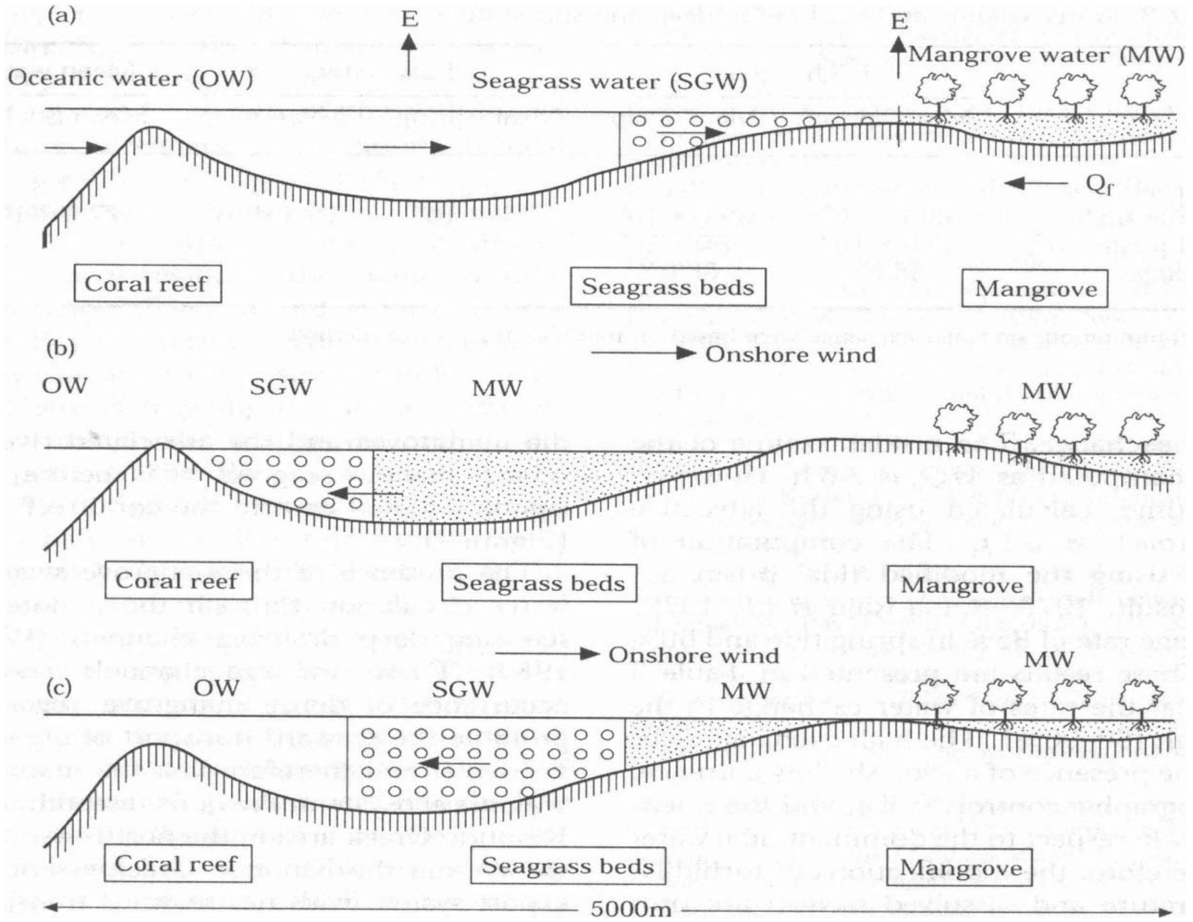

Fig. 13. Hydrodynamic link (or lack thereof) between a coral reef, seagrass bed and mangrove forest in Gazi Bay (Kenya) via the flux of oceanic water, seagrass-affected water and mangrove-affected water during a neap high tide (a), a spring low tide (b), and a neap low tide (c). E and Q_f refer to evaporation and freshwater input, respectively. Note that when the tide is rising (flood) during a neap high tide (a), the oceanic water (OW) moves over the coral reef into the seagrass habitat pushing the seagrass-affected water (SGW—open circles) toward the mangrove habitat and the mangrove-affected water (MW—dots) is restricted to the mangrove forest. In contrast, during a spring low tide (b), the oceanic water is restricted to the area offshore from the coral reef, the seagrass-affected water extends to the coral reef and the mangrove affected water covers the seagrass and mangrove habitats (but does not reach the coral reef). If only a neap low tide (c) occurs, the oceanic water penetrates farther into the lagoon than during the spring low tide and the seagrass-affected water remains in the seagrass habitat, not reaching the coral reef. Under these conditions, the mangrove-affected water extends somewhat into the seagrass habitat but not to the same extent as during the spring low tide. Source: Kitheka (1997). [Reproduced with permission from Academic Press/Elsevier].

VIII. Summary and Outlook

Fluid dynamics is an essential component of seagrass ecology as it affects every aspect of the plants and their habitats, from the smallest to the largest scales. Over the last decades, we have begun to understand how seagrass beds attenuate waves and currents. Now we begin a new phase of fine tuning previous findings and revising classical concepts. This is leading to exciting new developments such as (i) how currents interact with seagrass canopies as if the plants were part of a mixing layer instead of only a perturbation in the benthic boundary layer; (ii) the relative role of deposition and resuspension in seagrass beds, which may be quite dynamic; and (iii) how the aforementioned processes are affected by unsteady conditions. It is also becoming clear that not all seagrasses have the same biomechanical properties, and major differences exist in the extent to which different seagrasses influence, and are influenced by, water flow. Vegetated flows are amongst the most complicated and least understood types of water flow which makes this subject a great gateway for exciting new developments and advancements in science.

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Chapter 9

Nutrient Dynamics in Seagrass Ecosystems

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I. Introduction

A. Nutrients: Concept

The term 'nutrient' applies to any material that, taken into a living organism, serves to sustain it in its existence, promoting growth, replacing losses, or providing energy. In the framework of primary production ecology, the term 'nutrients' is usually understood as 'inorganic nutrients', that is, inorganic salts or ions that provide the elements necessary for plant survival, growth, and reproduction. Almost all the natural occurring elements are found in plant tissues; however, only a reduced number (17) are necessary for plant growth: these are called essential elements. They range from elements constituting the bulk of plant tissues (i.e. C, H, and O) to trace elements that are only required for a very specific biochemical function (e.g. Fe, Co). Except for, maybe, oxygen and hydrogen, all of them can be considered nutrients. However, the interest of plant physiologists and ecologists is usually in those anions or cations, which are likely to limit plant growth and production, i.e. those elements in which the supply is limited as compared with plant requirements.

B. Major Nutrients in the Sea: Nitrogen and Phosphorous

The synthesis of organic matter by primary producers can be viewed as a kind of stoichiometric reaction (in the sense that the reactants should be present at some definite proportions to give the final product). The following equation is often used as a reference for plankton production:

$$106\mathrm{CO_2} + 90\mathrm{H_2O} + 16\mathrm{NO_3^-} + \mathrm{PO_4^{3-}} \rightarrow \mathrm{C_{106}H_{180}O_{54}N_{16}P} + 150\mathrm{O_2} \quad (1)$$

According to the average elemental composition of seagrasses (Duarte, 1990), Eq. (1) could be roughly rewritten:

$$435\mathrm{CO_2} + 395\mathrm{H_2O} + 20\mathrm{NO_3^-} + \mathrm{PO_4^{3-}} \rightarrow \mathrm{C_{435}H_{790}O_{305}N_{20}P} + 522\mathrm{O_2} \quad (2)$$

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to obtain an oxygen release/carbon assimilation molar quotient of 1.2.

This equation will not be discussed further, as it is merely an orientation and disregards some basic facts, such as the (frequent) assimilation of ammonium instead of nitrate or the participation of the other essential elements. But it has the advantage of reminding us that plant growth is, to a certain extent, a process requiring specific 'reagents' at fixed proportions. It also highlights what we can consider the three major nutrients in the sea: carbon dioxide, nitrate (or the reduced form of inorganic nitrogen, ammonium), and phosphate. Inorganic carbon is, at least in bulk concentration, much more abundant than the other two in marine waters. Despite this, the importance of the dissolved inorganic carbon supply and its role in limiting or controlling plant growth is far from being completely elucidated. However, and since this topic is addressed elsewhere in this book (Larkum et al., Chapter 14), nutritional aspects related with carbon will not be further discussed here. Other elements considered as 'macronutrients' in agriculture or terrestrial ecology (K, S, Ca, and Mg) are probably not limiting in the marine environment, given the high concentration at which they occur. In any case, any reports examining their role in seagrass production are not known to us.

C. Other Minor Elements That Can Act as Nutrients

Micronutrients are considered the elements with very low concentration in plant tissues (in the order of hundreds of ppm or less), and probably the biologically most important are metals (Fe, Mo, Mn, and Cu). There are abundant data on concentrations of these elements in seagrass tissues (e.g. Ward, 1989; see also Ralph et al., Chapter 24), and about the plant or ecosystem response to them under some degree of pollution (e.g. Prange and Dennison, 2000), but unfortunately little is known about their physiological and ecological role under natural conditions.

Relatively recent experimental work has shown that iron can limit phytoplankton growth (e.g. Martin et al., 1994). Since iron additions have been shown to stimulate seagrass growth (Duarte et al., 1995), it could be supposed that iron can be a limiting element. However, the supply of trace metals can enhance nitrogen fixation, or can protect plant roots through binding the toxic sulphide ion (Chambers et al., 2001; Holmer et al., 2003), or even increase alkaline phosphatase activity, facilitating phosphorus uptake (see Marbà et al., Chapter 6). Therefore, the possibility of iron deficiency remains uncertain.

In view of the lack of research on micronutrients, the major focus of the rest of this chapter will be on nitrogen and phosphorus.

D. The Importance of Nutrients in Seagrass Ecology

The interest of seagrass ecologists in nutrient dynamics probably comes from two contrasting approaches. On the one hand, seagrass beds are sites of high, sometimes luxuriant, primary production. On the other hand, seagrasses frequently occur in oligotrophic waters (e.g. Mediterranean, tropical waters). The question of how seagrasses are able to sustain such a high primary productivity under conditions of low-nutrient availability has often puzzled the scientific community, just as it has for coral reefs. Moreover, the fact that seagrasses are rooted plants raises, in this context, the additional question about how such 'uncommon' marine plants perform under aquatic conditions.

On the other hand, the recent increase of nutrient concentrations in coastal waters, following the process of anthropogenic eutrophication, has promoted a considerable interest in the effects of increased nutrient levels on plant physiology and ecosystem functioning (see Walker et al., Chapter 23; Ralph et al., Chapter 24; Kenworthy et al., Chapter 25).

II. Nutrient Economy: Acquisition, Transport, and Storage

A. Nutrient Sources

In contrast to terrestrial plants, submerged aquatic vascular plants, including seagrasses, can take up nutrients not only through roots but also through leaves (Iizumi and Hattori, 1982; Thursby and Harlin, 1982, 1984; Short and McRoy, 1984; Stapel et al., 1996; Pedersen et al., 1997; Terrados and Williams, 1997; Lee and Dunton, 1999b). Except for *Phyllospadix*

Abbreviations: ABC – ATP binding cassette; tranport protein; ATP – adenine triphosphate; ATP'ase – a class of enzyme that hydolyzes adenosine triphosphate; δ^{15}N – ratio of ^{15}Nto^{14}N; DBL – diffusive boundary layer; DOP – dissolved organic phosphorus; POP – particulate organic phosphorus.

spp. and *Thalassodendron ciliatum*, seagrass root tissues are exposed to sediment pore water, which has usually much higher nutrient concentrations than the water column, and this makes a marked difference in nutrient acquisition relative to algae.

Water column and sediment pore water largely differ in geochemical characteristics, and, hence, in nutrient availability and turnover. In the water column, oxic conditions prevail, and nutrient concentrations are usually low, typically 0–5 μM for nitrate, 0–0.4 μM for phosphate and very variable (but generally lower for nitrate than ammonium). Phosphate is easily adsorbed to particles, which explains its lower concentration; however, it is considered that phosphate is biologically much more reactive, with residence times shorter than those of nitrogen species.

In pore water, most of the inorganic nitrogen is in the form of ammonium, with concentrations ranging from 1 to 1,000 μM, and probably more, while phosphate reaches up to 20 μM (Udy and Dennison, 1997a; Touchette and Burkholder, 2000) and nitrate is much more scarce. Nutrient availability in pore water largely depends on important biogeochemical processes, such as denitrification (which is important in terrigenous, moderately organic sediments; but see below), nitrogen fixation (occurring mostly in tropical areas) or phosphorus sequestration by carbonates and/or calcium, typical of biogenic sediments. These processes can cause nutrient imbalances, and, hence, seagrass growth limitation by specific elements determined by the nature of the sediment (e.g. Short, 1987).

Finally, it has to be taken into account that low molecular weight organic compounds can act as N and P sources. Concerning nitrogen, urea is an effective nitrogen source in seaweeds, but not in seagrasses. However, some amino acids (glutamic acid) can contribute to seagrass N nutrition (Bird et al., 1998). Concerning phosphorus, organic phosphorus, either as dissolved organic phosphorus (DOP) or particulate organic phosphorus (POP) can be a P source readily usable through hydrolysis by a number of forms of the enzyme alkaline phosphatase. Alkaline phosphatase activity has been found in seagrass leaves and roots (Pérez and Romero, 1993). However, the real role of phosphatase remains uncertain since the concentration of the substrate for these enzymes (monoester phosphate) seems to be very low, at least in natural freshwaters (Hernández, 1992).

B. Nutrient Uptake and Assimilation: Relative Role of Leaves and Roots

1. Leaf vs. Root Absorption Capacity

The putative ability of seagrasses to exploit the large nutrient pool of pore waters has led to the notion that this is the main source of inorganic nutrients for their growth. This has often been mentioned as an explanation of their success in colonizing vast areas, even in oligotrophic waters, and root tissues have been generally considered more important contributors of overall nutrient acquisition than leaves. There is, however, evidence that leaf tissues have higher nutrient uptake affinities than root tissues (see below) at low-nutrient availability (Pedersen et al., 1997; Lee and Dunton, 1999b), and several studies have indicated that nutrient uptake by leaf tissues contributed considerably to the total nutrient acquisition of seagrasses (Iizumi and Hattori, 1982; Short and McRoy, 1984; Pedersen and Borum, 1992; Stapel et al., 1996; Terrados and Williams, 1997; Lee and Dunton, 1999b; Lepoint et al., 2002b).

2. Uptake and Assimilation

Nutrient incorporation is a rather complex process, which includes two basic coupled steps: uptake and assimilation. Uptake is usually understood as the internalization of nutrients from the environment to the plant cells, while assimilation is the incorporation of such nutrients into the organic matter. Although the terms uptake and assimilation are sometimes used indistinctly, they are in fact very different steps in the process of nutrient acquisition.

In higher plants, inorganic nutrient uptake is brought about by a variety of plasma membrane transporters (H^+ ATPases, ABC transport proteins, etc.). Two different systems (low and high affinity) are involved, both in nitrate and ammonium uptake (Ourry et al., 1997; Grossman and Takahashi, 2001). Phosphorus is generally taken up using membrane-spanning proteins (H^+ATPase) as transporters (Muchhal-Umesh and Raghothama, 1999; Raghothama, 1999). However, despite the large body of knowledge on membrane pumps in terrestrial plants, the biochemical and molecular nature of uptake mechanisms (genes, proteins involved, etc.) have not yet been investigated in seagrasses, apart from a single study in *Z. marina* (Maramatsu et al., 2002). In contrast, data on nutrient uptake

Table 1. Compilation of published kinetic parameters of nutrient uptake. V_{max} is the uptake nutrient rate at saturating nutrient concentration, and Km is the concentration at which a rate of $V_{max}/2$ is reached. α is the uptake efficiency at low-nutrient concentrations.

Species	Nutrient	Organ	Km (μM)	V_{max}(μmol g^{-1} h^{-1})	α (l g^{-1} h^{-1})	Source
Zostera marina	NO_3^-	Leaves	23			Iizumi and Hattori (1982)
Phyllospadix torreyi		Leaves	8.69	46.67		Terrados and Williams (1997)
Thalassia testudinum		Leaves	2.2–38.5	3.7–6.5	0.15–1.68	Lee and Dunton (1999b)
Zostera marina	NH_4^+	Leaves		1.05–3.18		Short and McRoy (1984)
		Roots		0.88–2.93		
Zostera marina		Leaves	9.2	20.5	2.2	Thursby and Harlin (1984)
		Roots	104	211	0.5	
Thalassia hemprichii		Leaves	21–60	32–37	0.52–0.85	Stapel et al. (1996)
Amphibolis antarctica		Leaves	9.5–74.3	5.9–43.1	0.6–0.8	Pedersen et al. (1997)
		Roots	4.7	1.1	0.2	
Phyllospadix torreyi		Leaves	14.24	110.16		Terrados and Williams (1997)
Thalassia testudinum		Leaves	7.6–15	8.3–16.4	0.57–2.82	Lee and Dunton (1999b)
		Roots	34.4–765.5	7.9–73.3	0.03–0.3	
Zostera noltii	PO_4^{3-}	Leaves	12.1	43	1.1	Pérez-Lloréns and Niell (1995)
Thalassia hemprichii		Leaves	7.7–15	2.2–3.2	0.12–0.19	Stapel et al. (1996)
Thalassia testudinum		Leaves	11.9	1.9	0.23	Gras et al. (2003)
		Roots	3.7	0.57	0.10	

kinetics, although scarce, are available in the literature. Nutrient uptake rates are usually measured at various nutrient concentrations, plotted as a function of such concentrations and then kinetic parameters are derived using the Michaelis–Menten equation. Results from various uptake studies on several seagrass species showed that both leaf and root tissues were capable of significant nutrient uptake, although kinetic parameters were highly variable among species, and between different plant organs (Table 1). Ammonium seems the preferred form for N uptake, as shown by the lower uptake affinity for nitrate than for ammonium (Lee and Dunton, 1999b), and by the higher uptake rates for ammonium than for nitrate when both were present (Short and McRoy, 1984; Terrados and Williams, 1997; Lee and Dunton, 1999b; Lepoint et al., 2002b). These findings are consistent with the elevated cost of nitrate assimilation (Thacker and Syrett, 1972; Lara et al., 1987; Turpin, 1991 and see below).

Few phosphate uptake kinetic studies are available in the literature but they show a phosphate affinity in the same order of magnitude as that for ammonium, although data for phosphorus uptake were not always obtained for the same species as for nitrogen uptake (Table 1).

In general, much higher uptake affinities and uptake rates (higher V_{max} and/or lower Km) were observed for leaves than for roots, which is consistent with the nutrient concentrations of their respective surrounding waters. These nutrient uptake kinetics patterns seems to reflect plant adaptations to partition nutrient acquisition between two media with contrasting nutrient availability.

3. *Diffusive Boundary Layers*

At least two additional aspects have to be considered in relation to leaf nutrient uptake by seagrasses. First, the resistance to nutrient uptake induced by the unstirred boundary layer. The influence of diffusive boundary layers (DBLs) on several biological processes has received much attention (e.g. Denny and Wethey, 2001; Koch et al., Chapter 8; Larkum et al., Chapter 14), and it is known that, under certain conditions, it can curtail solute exchange. The relevance of such boundary layers in seagrass biology has been examined mostly related to inorganic carbon acquisition (e.g. Koch, 1994; James and Larkum, 1996; Larkum et al., Chapter 14); however, there is also some evidence of its importance for nutrients in aquatic macrophytes: for example, periodic stripping of the boundary layer by passing waves has been shown to increase nutrient uptake by a factor of 10 (Stevens and Hurd, 1997; Koch et al., Chapter 8).

4. Epiphytes

The second aspect to take into consideration is the potential interference of epiphytes in nutrient uptake by leaves. The presence of small organisms on the exchange surface surely adds complexity to the diffusive process. As epiphytes increase leaf roughness, they could reduce the thickness of the boundary layer under wave or current action, as well as increasing the boundary layer under unstirred conditions. However, since most of these epiphytes are algae, they also take up nutrients from water, thus creating a competitive interference. In any case, and as far as we are aware, these aspects have not been investigated in detail (see also Section IV.A, Koch et al., Chapter 8 and Borowitzka et al., Chapter 19).

5. Assimilation of N and P

Once nutrients have entered the cell, they can be immediately assimilated into organic matter or they can be stored in inorganic forms for further use. Since very low intracellular concentration of ammonium and nitrate have been reported (Invers et al., 2002), it has to be concluded that, in seagrasses, assimilation, at least for the species investigated, occurs shortly after uptake. Whereas for ammonium this is not surprising, given the fact of its known toxicity (van Katwijk et al., 1997), the lack of nitrate accumulation is in contrast to what happens in algae, where nitrate is one of the storage forms of N (Lapointe and Duke, 1984).

Ammonium assimilation takes place through the GOGAT pathway, i.e. formation of glutamine from glutamate and ammonium, catalyzed by glutamine synthetase (GS). This requires energy (1 ATP is needed for each glutamine synthesized). Ammonium assimilation occurs in both leaves and roots (and rhizomes), as indicated by in vivo and in vitro GS activity measurements (Pregnall et al., 1987; Kraemer and Alberte, 1993; Kraemer et al., 1997; Kraemer and Mazzella, 1999; Kraemer and Hanisak, 2000; Invers et al., 2002; species involved: *Zostera marina*, *Thalassia testudinum*, *Posidonia oceanica*, *Cymodocea nodosa*, and *Zostera noltii*).

Nitrate assimilation requires a previous step consisting of nitrate reduction to ammonium, which involves the participation of two enzymes (nitrate reductase and nitrite reductase) and NADH or NADPH; ammonium obtained by these reductions is then incorporated to organic matter via GOGAT. Measurements of the activity of the nitrate reductase in seagrasses (*Zostera marina* and *Halophila stipulacea*, Doddema and Howari, 1983; Roth and Pregnall, 1988; Touchette and Burkholder, 2001) have shown higher values in leaves than in roots, consistent with the relative availability of nitrate to both organs. Nitrate reductase activity is lower in seagrasses than in algae; this can be a consequence of an adaptation of seagrasses to the major use of ammonium as inorganic N source, a 'preference' afforded by the ready access to large ammonium pools in the sediment, either directly (through roots) or indirectly (ammonium release from pore water to the water column (see Marbà et al., Chapter 6)).

6. The Role of Leaves and Roots

The above-mentioned facts suggest that seagrasses have a certain plasticity in the acquisition of nutrients. Apparently, they have inherited many of the absorption mechanisms of flowering land plants from which they evolved at an early stage. However, in contrast to land plants and as in other hydrophytes, leaves may play a much greater role in nutrient uptake. The relative importance of leaves and roots in the acquisition process seems to be modulated according to environmental constraints. Available evidence suggests that, in very general terms (and with the obvious exception of species attached to rocky substratum, such as *Phyllospadix*), leaves and roots are equally important for nutrient acquisition. This is the conclusion for *Zostera marina* based on a numerical model (Zimmerman et al., 1987), and for

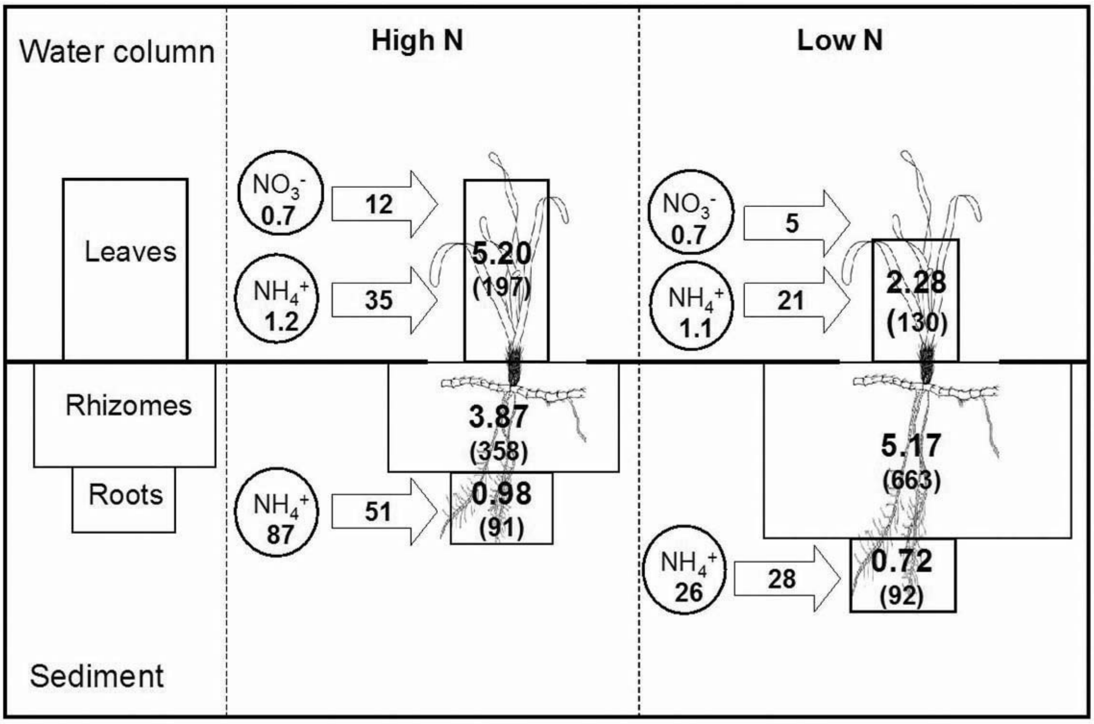

Fig. 1. Main compartments and fluxes in nitrogen acquisition in two *Thalassia testudinum* stands. Dissolved inorganic nitrogen concentrations (circles) are in μM, nitrogen in the different plant compartments (boxes; box size is proportional to N stock) are in g N m^{-2} and nutrient uptake (arrows) are in g N m^{-2} yr^{-1}; biomasses of each compartment (g DW m^{-2}) are also indicated in brackets. Despite the different pore water N availability, the relative contribution of roots vs. leaves in nutrient uptake is balanced and nearly equal at both sites. This is due to the different pattern of biomass allocation to above- and belowground plant parts. Redrawn from Lee and Dunton, (1999b), and data from Lee and Dunton (1999a).

Thalassia testudinum based on field work (Lee and Dunton, 1999b, among others) (Fig. 1).

This equal importance of leaves and roots in nutrient acquisition seems in contradiction with the differences in nutrient concentration between pore water and water column. However, it has to be remembered that nitrogen assimilation and, to a lesser extent, uptake depend on both energy (ATP) and electrons (NADH/NADPH) supplied by photosynthesis or respiration. As assimilation in the belowground organs implies the transport and use of photosynthates, largely as sucrose, metabolism can service uptake better in leaves than in roots, especially under low light conditions (Zimmerman et al., 1987). Moreover, uptake and assimilation largely depend on biomass or, more directly, on the surface area of plant material interacting with the surrounding water. Yet it is known that leaf area index of seagrasses can reach very high values (15–20, Buia et al., 1989, and unpublished data on *Posidonia oceanica*). Following the only comparative data available so far (Pérez-Lloréns, 1991 in *Zostera noltii*), leaf surface area exceeded by a factor of 10–30 that of roots. This is probably not the rule, but points to the importance of the biomass allocation to aboveground vs. belowground organs as an adaptive strategy for optimization of nutrient acquisition (see below).

It has also to be taken into account that leaves and roots do not act independently in nutrient acquisition. For example, high ammonium supplied to leaves caused a significant decrease in the maximum ammonium uptake rates by roots in *Zostera marina* (Thursby and Harlin, 1982). However, in *Ruppia maritima*, uptake of phosphate and ammonium by leaf tissues was affected by supply of these nutrients to the root tissues, but uptake by roots was not affected by the availability of these nutrients in water column (Thursby and Harlin, 1982, 1984). Finally, interaction among nutrient acquisition and community-level processes (e.g. herbivory, see Valentine et al., 2004; Valentine and Duffy, Chapter 20) should also be considered in order to fully understand seagrass nutrient metabolism.

C. Nutrient Conservation Strategies: Internal Recycling and Storage

A remarkable feature of seagrasses is their efficient use of nutrients to attenuate losses, through leaf abscission and loss, and to buffer environmental fluctuations in nutrient availability. In effect, on the one hand plants resorb nutrients (often called nutrient reclamation) from old tissues and use them in other plant parts. On the other hand, they can take up nutrients in excess of immediate metabolic needs, which is often known as 'luxury consumption', and store them in different forms, before or after assimilation. These strategies reduce the dependence of seagrasses on the external medium, and are shared by other primary producers: some algae exhibit luxury consumption (e.g. Chapman and Craigie, 1977), and terrestrial plants, much closer to seagrasses, exhibit nutrient storage and reclamation (Chapin and Kedrowski, 1983; Escudero et al., 1992; Reich et al., 1995, among others).

Little is known about specific mechanisms involved in nutrient resorption; Invers et al. (2002) proposed that the main form of transport of resorbed nitrogen would be amino acids. However, the role of nutrient resorption in seagrass nutrient economy has been repeatedly evaluated (Pedersen and Borum, 1993; Alcoverro et al., 1997; Mateo and Romero, 1997; Stapel and Hemminga, 1997; Hemminga et al., 1999; Alcoverro et al., 2000; Stapel et al., 2001; Invers et al., 2002; these works mainly refer to *Zostera marina* and *Posidonia oceanica*). Most of these authors have used a nutrient mass balance approach, with different degrees of detail in sampling and/or in elaboration of results. This approach estimates resorption as the difference in nutrient mass between the leaf (or tissue) having the maximum and the oldest leaf, usually having the minimum, or alternatively, recently shed leaves. However, this has some methodological uncertainties, including the lack of knowledge about leaching (that seems to be small: see Borum et al., 1989 and Pedersen and Borum, 1992 but these works refer only to *Zostera marina* in a small geographic area) and the adequacy of the material taken as reference for nutrient losses, i.e. if standing leaves are used, resorption may not have been completed yet and if shed leaves are used, microbial processes may have already changed nutrient content. The recent use of isotopic tracers seems to be a promising tool not only to better evaluate the amount of nutrients resorbed, but also to determine how they are re-used (Pedersen et al., 1997; Stapel et al., 2001; Marbà et al., 2002; Lepoint et al., 2002a). So far, however, the results of these works seem to agree, at least in general terms, with those using the mass balance approach (compare, for example, Lepoint et al., 2002a and Alcoverro et al., 2000 for *P. oceanica*; and Stapel et al., 2001; Stapel and Hemminga, 1997; and Martins and Bandeira, 2001 for *Thalassia hemprichii*).

The values for nutrient resorption obtained in the works cited above range from 10% to 50% of annual N requirements, and slightly more for P requirements. Average values of 20.4% and 21.9%, for nitrogen and phosphorus, respectively, are mentioned in the review by Hemminga et al. (1999). These amounts are, in general, lower than those reported for terrestrial plants (see, for example, Chapin and Kedrowski, 1983; Aerts, 1996), but represent a substantial contribution to the annual nutrient budgets of seagrasses. Resorption capacity could be linked to leaf longevity, and thus long life-span of leaves could be viewed as an advantage in oligotrophic waters. This is the case for *P. oceanica*, which has the highest resorption rates evaluated so far (Alcoverro et al., 2000; Lepoint et al., 2002a), and whose leaves have very long life-spans (up to 200–300 days: Romero, 1989; Duarte, 1991). This resorption hypothesis, although consistent with that which occurs in terrestrial plants (e.g. Escudero et al., 1992), has not been fully demonstrated in seagrasses (Hemminga et al., 1999).

Storage is an obvious adaptive response to fluctuation in nutrient availability, particularly in large perennial plants. Both leaves and rhizomes can act as storage sites in seagrasses, with their relative importance depending on the local nutrient availability regime, the species physiology, and the life-span of those organs (Pirc and Wollenweber, 1988; Pedersen and Borum, 1993; Pérez et al., 1994; Kraemer and Mazzella, 1999; Invers et al., 2002).

Nitrogen can be stored in different forms, the major form being amino acids, especially asparagine (Udy and Dennison, 1997b; Udy et al., 1999). However, soluble protein also accounts for an important part of nitrogen storage (Murray and Larkum, 1991), as well as non-soluble compounds, while inorganic compounds seem of minor, if any, importance

(Invers et al., 2002). Very little is known about the form in which phosphorus storage occurs.

Storage can take place at different time-scales. In the short term, seagrasses can take up nutrients, and use them several hours to days later. For example, *Z. marina* has the ability to reduce nitrate regardless of time of day, thus taking advantage of infrequent, short-term night pulses of nitrate. This short-term storage capacity also allows the species to reduce nitrate during storms, in which nitrate availability increases but the turbidity of the water severely limits light reaching the canopy (Roth and Pregnall, 1988; Burkholder et al., 1994). Such behavior would require redirection of carbohydrates from storage reserves to the production of the energy and carbon skeletons needed to reduce nitrate and form amino acids (Turpin, 1991; Ferrario-Méry et al., 1997).

However, probably the best documented storage behavior is that related to the seasonal changes in nutrient availability. In most temperate areas, nutrient availability varies seasonally, and is usually uncoupled to light availability and to optimal temperature conditions. Thus, during the nutrient 'rich' period, plants take up nutrients, probably assimilate them (at least in the case of N), and store them in leaves and/or in rhizomes (Pellikaan and Nienhuis, 1988; Alcoverro et al., 1995, 1997; Kraemer and Mazzella, 1999), to be used during the nutrient 'poor' period. Less is known about possible interannual storage mechanisms, although the minimum value of N content in rhizomes, i.e. that reached after the use of reserves, changes from year to year (Alcoverro et al., 2000); there is thus the possibility that some stored N remains in the rhizomes after a 'good' year, to be used the year after.

D. Nutrient Transport

Given the participation of both leaves and roots in nutrient acquisition, it could be supposed that transport of nutrients would not be as important as in terrestrial plants. However, internal nutrient demand is by no means coupled to nutrient acquisition (neither spatially nor temporally), and there are a number of processes requiring nutrient transport between different parts of the plant, both over relatively short distances (for example, from cell to cell, from the leaf blade to the basal meristem, etc.) and over relatively long distances (relocation of nutrients from senescent leaves before abscission, mobilization of nutrients stored in rhizomes, transport from intercalary shoots to apical shoots, etc.). Transport should therefore be considered as an essential part of seagrass nutrient economy, and a key aspect in its functional clonal integration.

Surprisingly, the research effort devoted to the study of nutrient transport in seagrasses is notoriously sparse, especially when compared to the advances made in terrestrial plants. Issues such as the physiological basis of transport, the factors determining source/sink shifts within the plant, the biochemistry of the transported substances, or how resources are shared between ramets have been addressed only preliminarily or remain simply unexplored.

Cell-to-cell (symplastic) transport, or transport by diffusion in the extracellular space (apoplastic) can account for short-distance movements of solutes. For example, in *Syringodium isoetifolium* no connections (i.e. plasmodesmata) between adjacent epidermal cells nor between epidermal and mesophyll cells were observed, suggesting exclusively apoplastic transport (Kuo, 1993). However, in other species such as *Zostera muelleri* and *Phyllospadix* sp. plasmodesmata are present connecting epidermal cells among them and with mesophyll cells (Kuo, 1993; Kuo and Stewart, 1995), allowing symplastic nutrient transport.

These cell-to-cell mechanisms are excessively slow for long-distance transport (i.e. above 10 cm), at least in terrestrial plants (Mengel and Kirkby, 2001), where long-distance transport is achieved via the vascular system, basically through the xylem system (acropetal transport) but also through the phloem system (multidirectional transport). It is obvious that water pressure gradients created by water evaporation at the leaves surfaces do not exist in seagrasses, and xylem transport, if any, should be driven differently. To date, the only known alternative is through the active accumulation of solutes in the plasma membrane of xylem parenchyma cells, which induces a pressure (root pressure) from the water tending to enter the xylem (e.g. Steudle and Peterson, 1998). Although this mechanism seems to have a certain role in terrestrial plants whose transpiration is inhibited, it seems unlikely that it plays an effective role in seagrasses, due to the high salt content of seawater. Moreover, it has to be remembered that xylem is generally reduced in seagrasses (Kuo, 1993; Kuo and Stewart, 1995). Thus it would seem that long-distance transport should be predominantly achieved via the phloem system. The phloem, although classically described as the vascular system responsible for the distribution of assimilates all over the plant (multidirectional transport), allows the translocation of the so-called phloem mobile nutrients (Marschner et al., 1996, 1997). The driving force for phloem transport is the turgor pressure gradient (created by differences in solute potential between source and sink areas of the plant, Mengel and Kirkby, 2001). Its role as the main transport system in seagrasses is supported by morphological evidence, such as the weak wall ingrowths found in phloem parenchyma cells facing the sieve tubes (conduits made of connected living cells lacking a nucleus), which suggests that these parenchyma cells may play an important role in solute transport (e.g. *Phyllospadix* sp., Kuo and Stewart, 1995).

Resource sharing between different shoots (or ramets) seems to be another essential component of seagrass nutrient economy, as it is for clonal terrestrial plants (e.g. Herben and Suzuki, 2001), and it also requires an efficient transport system. Internal redistribution of nutrients can allow efficient management of these key elements, conducting them to the sites with maximum demand independently of the specific sites of acquisition (see Marbà et al., 2002). However, despite its apparent importance, this mechanism has been only rarely investigated, although indirect evidence of such integrated behavior has been obtained (e.g. Tomasko and Dawes, 1989; Pedersen and Borum, 1992; Terrados et al., 1997b). Using short-term experiments (4 days) with stable isotopic tracers, Marbà et al. (2002) showed that, developing ramets of several species may receive up to 40% of their nitrogen requirements from the neighboring ones. Resources traveled preferentially from older to younger (apical) shoots and covered distances up to 80 cm in this 4-day period. It has to be pointed out that resources are shared between ramets almost immediately after incorporation, meaning that retranslocation affects primary products of synthesis. This extends and reinforces the concept of integration for seagrass ramets in the framework of nutrient metabolism. Further research efforts are obviously needed in that direction.

III. Nutrient Fluxes in Seagrass Ecosystems

In seagrass beds a variety of processes driving the flux of matter within the ecosystem and between the ecosystem and the rest of the marine environments take place (see a simplified representation of these processes for N in Fig. 2). Here we briefly summarize the nutrient fluxes from an ecosystem perspective; as it is true that N and P fluxes often work in parallel with C fluxes (treated elsewhere in this book, see Mateo et al., Chapter 7, and Marbà et al., Chapter 6), we will focus only on specific aspects of key importance to understand nutrient–seagrass interactions.

A. Nutrient Inputs to Seagrass Ecosystems

A first input of nutrients takes place when the dissolved salts of N and P are extracted from the water by the complex of leaves plus epiphytes, and, eventually, other micro- and macroalgae attached to the rhizomes or living in the sediment surface. The nutrients available in the water for plants include those coming from outside the seagrass bed (what we can consider 'new' nutrients) and also those released during the process of leaf decay or regenerated by benthic remineralization and release ('recycled' nutrients). The importance of dissolved forms in the overall nutrient budget of the system will depend on their mean concentration, the fluctuations around this mean, and on the turnover (or residence time) of the water in the seagrass bed.

A second input of nutrients is sedimentation of seston, whose constituents include variable amounts of organic N and organic and inorganic P. Seston is an important nutrient source in seagrass ecosystems, in part because seagrass leaf canopies act as particle traps, as they induce relatively calm hydrodynamic conditions facilitating sedimentation (e.g. Gambi et al., 1990; Worcester, 1995, among others; see also Marbà et al., Chapter 6; Koch et al., Chapter 8); this implies that N and P inputs from the seston are much higher under plant canopies than in comparable bare sediments.

Although the data concerning this nutrient flux are relatively scarce, it seems to be at least as important as that from dissolved nutrients uptake in the ambient water (Risgaard-Petersen et al., 1998). It has to be acknowledged that the estimate of net nutrient inputs through sedimentation is a rather difficult task, due to a combination of reasons including spatial and temporal heterogeneity, the complexity of the process itself (balance between sedimentation and resuspension), and the fact that part of the settled particles are originated from the bed. Using different approaches, estimates of net inputs of between 0.3 and 60 g N m^{-2} yr^{-1} have been proposed (Harlin et al., 1982; Kenworthy and Thayer, 1984;

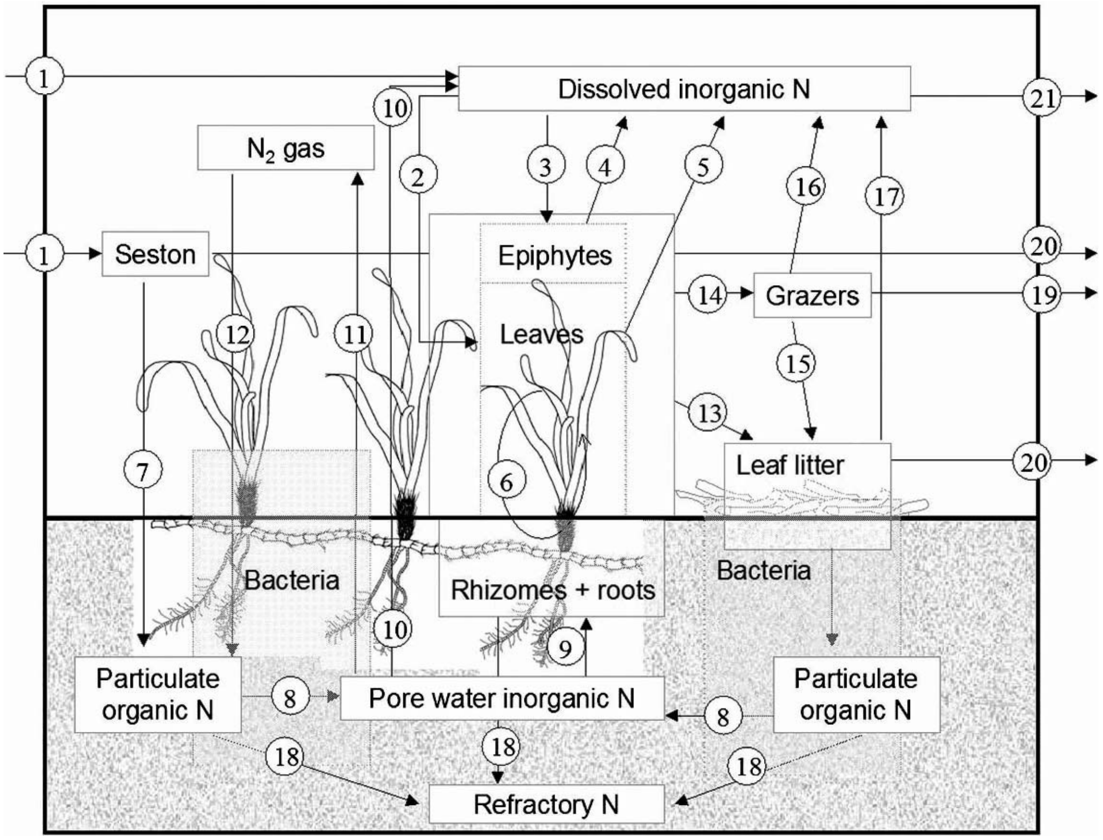

Fig. 2. Diagrammatic representation of the main fluxes of N in a seagrass meadow. Values for these fluxes are given in Table 2. To avoid complication, some fluxes have been omitted or simplified, among them: the processes of uptake and regeneration in the water column, nitrification (see Chapter 6, Marbà et al.,) and nitrate uptake by the sediment, the dissimilatory reduction of nitrate to ammonium (that seems to be important – Boon et al., 1986b; Caffrey and Kemp, 1990), the efflux of dissolved organic nitrogen from the sediment (Eyre and Ferguson, 2002) and the resuspension of sediment particulate N (see for example Miyajima et al., 1998). Some compartments are not represented, despite the fact that they can play some role in the N fluxes (suspension-feeders, meiofauna, infauna, etc.).

Almasi et al., 1987). More recently, and using sediment traps, Gacia et al. (2002) estimated a net input to the sediment of 13.4 g N m^{-2} yr^{-1} and 2.01 g P m^{-2} yr^{-1} in beds of *Posidonia oceanica* in the Western Mediterranean. These values are relatively high, of the same order as the annual growth needs of the seagrass. However, probably not all these amounts can be used by the plant. A part of N and P is in refractory forms, and is incorporated in the sediment sink (see below), while the rest decomposes, releasing inorganic nutrients to pore water. This decomposition can be stimulated by the efflux of oxygen from seagrass roots (see Kuo and den Hartog, Chapter 3; Borum et al., Chapter 10), which creates oxic or semi-oxic microenvironments in the rhizosphere. However, the consequences of this for nutrient cycling and availability have not been evaluated (but, see below, aspects related to denitrification).

Inorganic particles (e.g. carbonates) can also dissolve within the sediment, due to specific conditions such as low pH, and release small amounts of P. Nutrients in the pore water can be taken up by the roots, or diffuse into the water column.

In addition to passive sedimentation, suspension-feeders inhabiting the seagrass bed can actively capture particles, incorporating the associated nutrients into the general material flux of the seagrass ecosystem. The role of the suspension-feeders in the overall nutrient budget of the seagrass community has only rarely been evaluated, but seems very important in certain areas (see, for example, Lemmens et al., 1996), where these organism are the most abundant, while their role is only minor in others

Table 2. Tentative values for the fluxes represented in Fig. 2. For each flux, whenever possible, a range of values found in the literature is given, as well as a reasonable average, which has been computed excluding outliers. Data are in g N m^{-2} yr^{-1}, except where indicated as percent of annual N demands for growth (%). In those cases (%), the average has been estimated applying the percentage to the seagrass annual demand, which can eventually be somewhat unrealistic. This table does not present an exhaustive literature review, and it is only aimed at providing a very rough estimate of the order of magnitude of the main exchanges between compartments from the point of view of N dynamics. In a few cases, no reliable estimates are available.

Flux number	Flux description	Average	Range	Source
	Primary producers demand[a]			
	Epiphytes	11	2–23	From data in Koch and Madden (2001), Cambridge and Hocking (1997), Nelson and Waaland (1997), and Alcoverro et al. (1997)
	Seagrass	30	3–90	Estimated combining data in Duarte (1990) and Duarte and Chiscano (1999)
1	Nutrient import though advection (dissolved and particulate)	–	–	
2	Nutrient uptake by seagrass leaves	12[b]	26–47	*T. testudinum* (Lee and Dunton, 1999b)
			2.5	*P. oceanica* (Lepoint et al., 2002b)
3	Nutrient uptake by epiphytes	–	–	
4	Epiphytes leaching	–	–	
5	Leaf leaching	<1	1–4%	These data refer to P (see text)
			<10%	Borum et al. (1989)
6	Internal recycling	5	10–50%	Includes resorption, storage, re-use, etc. See text for references
7	Sedimentation	15	0.3–60	See text for references
8	Ammonification	114	18–176	*Z. capricorni* (Boon et al., 1986a)
			7–1069	*P. oceanica* (López et al., 1995)
			26–38	*T. testudinum*–E. acoroides (Williams, 1990)
			123–136	*Z. marina* (Caffrey and Kemp, 1990)
9	N uptake by seagrass roots	12[b]	28–51	*T. testudinum* (Lee and Dunton, 1999b)
			3.3	*P. oceanica* (Lepoint et al., 2002b)
10	Inorganic N release by sediment	1	0.53–1.56	Mixed tropical beds (Erftemeijer and Middleburg, 1995)
			5–20	*E. acoroides* (Holmer and Olsen, 2002)
			1.2	*Z. capricorni* (Eyre and Ferguson, 2002)
			0.3–0.5	*T. hemprichii* (Miyajima et al., 2001)
			1.9	*T. testudinum* (Ziegler and Benner, 1999)
11	Denitrification	<1	0.05–0.7 (up to 3.6–18)	Average for the lowest, most frequent range; see text for references
12	Nitrogen fixation	1–10	0.1–2.5	Temperate seagrasses (see text for references)
			2.7–15	Tropical seagrasses (see text for references)
13	Leaf fall	20[c]		
14	Leaf consumption by herbivores	4[d]	<1–90%	
15	Feces production	3		Estimated from the assimilation efficiency for N given by Thayer et al. (1982)
16	Regeneration by herbivores	4	1.9–6	*T. hemprichii* (Koike et al., 1987)
17	Regeneration during leaf litter decay	8	10–46%	See text for references

[a] Plant and epiphyte demands have been estimated as the product of annual primary production and their respective average N content.

[b] Average uptake by leaves and rhizomes has been estimated assuming that external demand is met equally by uptake of leaves and roots (see justification in the text). External demand is the annual demand minus the internal recycling.

[c] This flux has been estimated as the total N demand minus the part ingested by herbivores (flux 14), and this is multiplied by 0.74, which is the average fraction of N remaining in falling leaves, relative to living ones (estimated from data in Duarte, 1990 and Hemminga et al., 1999).

[d] Consumption was assumed to be, on average, 15% of primary production; to estimate N flux, the fact that some herbivores prefer old, nutrient-poor leaves has not been considered.

(e.g. in beds with poor epifauna; see also Bell et al., Chapter 26).

A third source of nitrogen ('new' nitrogen) in seagrass beds is nitrogen fixation. Nitrogen fixation occurs in both the phyllosphere and the rhizosphere, being, apparently, more important in the latter than in the former. Cyanobacteria and other prokaryotes are responsible for this fixation activity. The contribution of nitrogen-fixing organisms to the nutrient budget of the bed has mostly been evaluated in tropical areas, where it accounts for inputs in the range of 2.7–15 g N m^{-2} yr^{-1} (Capone and Taylor, 1980; O'Donohue et al., 1991; Moriarty and O'Donohue, 1993; Blackburn et al., 1994). Fewer data exist for temperate beds, where, apparently, N-fixation is less important (Capone, 1982; Welsh et al., 1996; McGlathery et al., 1998, between <0.1 and 2.5 g N m^{-2} yr^{-1}).

The coupling of nitrogen fixation to other biological processes in the root layer (e.g. Welsh et al., 2000; see also Marbà et al., Chapter 6) and its contribution to the nitrogen economy at a regional scale (e.g. Béthoux and Copin-Montégut, 1986) are promising fields for future developments.

B. Nutrient Losses from the Plant

Nutrients that have been incorporated into seagrass tissues can be lost by the following processes: leaching, leaf fall, and consumption by herbivores.

Significant amounts of dissolved nutrients are released by seagrass leaves (McRoy and Goering, 1974; Fresi and Saggiomo, 1980; Penhale and Thayer, 1980; Brix and Lyngby, 1985; Pérez-Lloréns et al., 1993), with values typically being between 1% and 4% of the phosphorus absorbed by the roots (Hemminga et al., 1991). As far as we are aware, this nutrient release has not been fully investigated, and it probably has a double origin: losses from living and healthy tissues and leaching of soluble compounds from senescing leaves. This flux is generally small, compared with other fluxes in the ecosystem, and probably an important part of the nutrients released are used by epiphytes.

Leaf fall is probably the most important process by which seagrasses lose nutrients. The timing and rate of leaf fall vary greatly between species, but in any case the falling leaves have considerable amounts of N and P. Available evidence indicates that N and P content in old leaves, or in recently fallen leaves, are considerably lower than that of newly growing leaves, and this greatly depends (if we accept that nutrient leaching is relatively small) on the resorption efficiency. Typically, fallen leaves have between 25 and 90% of their original nutrient content, with an average of, approximately, 75% (inferred from data of Hemminga et al., 1999). The fate of these nutrients will be discussed later.

Finally, a part of the leaf biomass can be removed by grazers. Although grazing activity is analyzed exhaustively elsewhere (see Valentine and Duffy, Chapter 20), it can be said that in most of the world's seagrass beds grazers have little influence on nutrient fluxes. This is based on the fact that grazing removal of leaf biomass is usually less than 15% of primary production (Cebrián and Duarte, 1998). In addition, herbivores show preferences towards the oldest tissues, having less nutrients. However, several facts should be considered that further complicate the assessment of the importance of grazers on nutrient fluxes. Thus, the preference of herbivores for the old tissues can curtail nutrient resorption by the plant; moreover, this preference seems to maximize epiphyte ingestion, in which a large amount of nutrients concentrate.

In turn, probably only a minor part of the nutrients in leaves and epiphytes ingested by herbivores will be incorporated into the consumer biomass, due to the low assimilation efficiency of herbivores (although scarcely measured for nutrients: Thayer et al., 1982; Velimirov, 1984) or released in soluble inorganic or organic labile compounds. Therefore, most of these nutrients will end up, via feces, in the detritus pool, indicating that the main role of herbivores in this respect is to transfer N and P from the plant to the decomposers food web. However, the impact of grazers on seagrass nutrient economy will depend on a key aspect of behavior: thus, species inhabiting permanently the seagrass bed (e.g. sea urchins, gastropods, some fishes) will cause mostly nutrient losses from the plant, limiting internal recycling (resorption from old leaves) and increasing external recycling (through decomposition, see below), but will probably increase only marginally nutrient export from the ecosystem (i.e. a nutrient in soluble form or in detritus is more readily exported than a nutrient in a leaf). In contrast, species feeding in the bed but living or resting elsewhere (water fowls, sirenidae, turtles, and some fishes: Thayer et al., 1982; Preen, 1995) induce a net nutrient loss from the ecosystem, increasing the dependence on external nutrients or, what is the same, increasing the new to recycled production ratio (see below).

A final word of caution when considering the role of herbivores in nutrient fluxes has to be said. While the general view of low and moderate grazing seems to be the rule, an increasing number of cases of intense grazing activity, and even of overgrazing events, have been reported, by fish, sea urchins, and water fowl (see Valentine and Heck, 1999, for a review, and Valentine and Duffy, Chapter 20). In all these situations, herbivores can become the major force driving key nutrient fluxes (nutrient losses from the plant and/or nutrient export outside the seagrass bed).

C. Nutrient Regeneration Within the Ecosystem

Nutrients that have been incorporated into the leaves can then follow three pathways: they can be retranslocated to other plant parts (young leaves, rhizomes, etc.), they can be leached and they can remain in the leaf tissue until leaf fall occurs. The first two possibilities have been already addressed; we will focus here on the third one.

Leaf litter is probably the main source for regenerated nutrients in the seagrass bed, and decay (or decomposition) is the process by which nutrients are returned to soluble form. Estimates of the importance of nutrient regeneration through leaf decomposition in the nutrient budget are scarce. Reported values are in the range 10–46% of the N annual demands for leaf production (Walker and McComb, 1985; Romero et al., 1992; Mateo and Romero, 1997; species studied: *Amphibolis antarctica*, *Posidonia australis*, *Posidonia oceanica*, and *Cymodocea nodosa*), and slightly higher for P where data were available. These values depend, on the one hand, on the seagrass capacity to absorb these nutrients, and, on the other hand, on the export rates (see below). The range of values are much wider when considering other communities or geographical areas, where export rates can be from near zero (e.g. coastal lagoons) to near 100% of the primary production (e.g. surf zones, such as those occupied by *Phyllospadix* spp.; see below and also Mateo et al., Chapter 7).

Nutrient dynamics during the decomposition process is rather complex, and clearly differs from the kinetics of weight loss, which follow a typical negative exponential (Olson, 1963). Classically, three phases are distinguished during leaf decay: (i) leaching, (ii) microbial, and (iii) refractory phases (Kristensen, 1994; Valiela, 1995; see also Mateo et al., Chapter 7). During the leaching phase, nutrients are released in very labile forms, and some of them are rapidly incorporated by microbes coating the leaf detritus. When all labile substrates have been used, bacteria begin to attack the dead leaf tissues using exoenzymes; this implies the release of nutrients in either inorganic or organic labile forms, part of which are again incorporated by bacteria. Finally, in the refractory phase, decay is very slow, although in some cases N-rich compounds are still being decomposed, while most carbon, bound in condensed humic compounds, is not (Kristensen, 1994). There is probably no common pattern of nutrient content change during leaf decay (Peduzzi and Herndl, 1991; Romero et al., 1992; Kristensen, 1994; Mateo and Romero, 1997; Miyajima et al., 1998; Holmer and Olsen, 2002; see Fig. 3); however, the contention of Harrison (1989) about nitrogen not accumulating in leaf detritus seems to be valid, at least in general terms. Nutrients released in dissolved forms can be re-used by seagrasses or other primary producers; those incorporated by bacteria can be remineralized after detritus ingestion by detritivores; and, finally, those bound to refractory compounds in detritus can be either exported or stored as organic nutrients in the seagrass sediments. In addition, the fact that the C:N and C:P ratios of detritus are considerably higher than those of the bacterial biomass suggests possible nutrient incorporation by bacteria from sources other than the detritus and/or nutrient limitation of bacterial growth (e.g. López et al., 1998). However, experimental data indicate that nutrients in the detritus are more important in controlling decay than nutrients in the water column (Pérez et al., 2001).

D. Nutrient Losses from the Bed: Export

In contrast to most terrestrial systems, seagrasses suffer substantial nutrient losses through the export, sometimes massive, of leaf detritus. An important part of seagrass production can exit the seagrass bed, transported by waves and currents, to adjacent ecosystems including terrestrial, inter-tidal, and subtidal environments (see Bell et al., Chapter 26).

Export rates reported in the literature present an extremely wide range (from 0% to 90% of the leaf production: see Mateo et al., Chapter 7). Data about the amount of nutrients exported in this way are

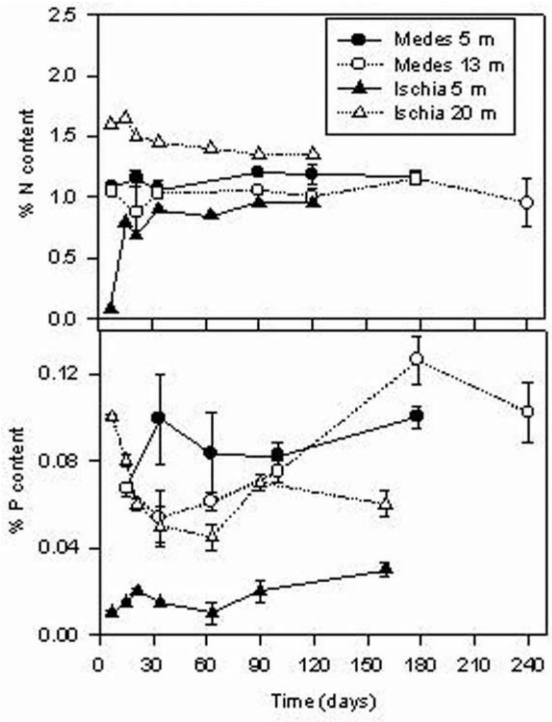

Fig. 3. N (upper) and P (lower) content time course during decomposition of leaf detritus of the Mediterranean seagrass *Posidonia oceanica.* Senescent leaves were incubated in 1 mm mesh litter bags in two geographical areas (Ischia, Italy, and Medes Islands, Spain) and at two depths. The results are relatively heterogeneous, but it seems clear that neither N nor P accumulation occurs during the refractory phase. Redrawn from data in Mateo and Romero (1997) and Romero et al. (1992).

much scarcer, but it has to be remembered that carbon and nutrients follow parallel fluxes, and, to obtain a rough estimate, the export data mentioned can be transformed into nutrient export fluxes using C/N or C/P ratios in leaf detritus, or their respective N and P content. Romero et al. (1992), Pergent et al. (1994), Mateo and Romero (1997), and Pérez et al. (2001) estimated the yearly losses of nutrients from beds of *P. oceanica* and *C. nodosa* in the Mediterranean, between 3% and 53% of total annual nutrient requirements, with values decreasing with depth. N export rates up to 82% of total N assimilated have been reported in shallow water *Z. marina* beds (Risgaard-Petersen et al., 1998). This is due to the importance of hydrodynamism as the main force driving litter export. These few data highlight the relevance of this latter process (see Koch et al., Chapter 8). In addition, it has to be said that the values reported refer almost exclusively to macrodetritus, while microdetritus (<1 mm), produced during fragmentation of leaves, or by grazers activity, have been only very rarely studied; yet microdetritus can be involved in important nutrient fluxes (Bach et al., 1986; Pellikaan and Nienhuis, 1988).

However, for a better understanding of the export process, it has to be taken into account that the detritus pools suffer two concurrent processes: export, a probabilistic process linked to a given regime of storms and/or currents, and decay, a more continuous and deterministic one. These processes clearly interact: the lower the decay rates are, the higher is the export probability (Pérez et al., 2001). Moreover, other factors, such as the degree of coupling between leaf fall and hydrodynamic events or the buoyancy of leaf detritus influence the litter stock dynamics and, hence, the nutrient export rate.

Keeping in mind the variability of the export process, it can be stated that, on average, it represents the main nutrient flow out of the bed, since losses in dissolved form and burial (see below) represent only marginal or small outputs. Thus, export of leaf material (and attached epiphytes, and, eventually, macroalgae) seems to be of major importance for the bed nutrient budget and deserves further research, not only in evaluating its magnitude but, mostly, in elucidating its controls, the possible feed-backs with eco-physiological processes and the interactions with other ecosystem fluxes.

Export of biomass and nutrients functionally links the seagrass beds to other coastal ecosystems. The analysis of the importance for such systems of the seagrass materials is beyond the scope of this chapter (but see Kenworthy et al., Chapter 25 and Bell et al., Chapter 26).

E. Other Losses: The Sediment Sink

1. Types of Processes

The sediment is probably the largest pool of nutrients in the seagrass bed. Most of the nutrients here occur in particulate form, in seagrass tissues (roots, rhizomes), as detritus or as inorganic particulates. A part of the N and P in these forms is released to pore water as soluble salts, and then absorbed by roots (or microalgae, or bacteria), or in turn released to the water column. However, another part is lost to the general ecological nutrient cycle, at least at the scale of tens of years, or probably more frequently;

processes accounting for such losses are basically three: (i) denitrification (only affecting N), (ii) sequestration in non-soluble minerals (only affecting P), and (iii) burial in organic refractory compounds (affecting both N and P). Seagrass beds are therefore potential nutrient sinks, and this is relevant not only for the seagrass ecosystem itself but also for the biogeochemical cycles of the elements and/or for the nutrient dynamics of coastal ecosystems (see also Marbà et al., Chapter 6).

2. Denitrification

In denitrification, nitrate, nitrite, and nitrous oxide are reduced by bacteria to $N_2(g)$ that fluxes off the sediments to the atmosphere. The process takes place in oxygen-depleted sediment layers, and requires an adequate supply of nitrate, etc, and organic matter. Nitrifying aerobic bacteria oxidizing ammonium (typically derived from biotic activity, i.e. ammonification) are recognized as the main agents providing these oxidised nitrogen sources in littoral marine sediments (Seitzinger, 1988). Since denitrification requires a close coupling of aerobic and anaerobic processes, it would seem that the seagrass rhizosphere, where oxic microlayers caused by oxygen release from roots intermix with hypoxic or anoxic zones (Kuo and den Hartog, Chapter 3), constitutes an optimal environment where it can take place (Hemminga and Duarte, 2000). Indeed, some evidence indicates that denitrification is higher in seagrass beds than in neighboring bare sediments (e.g. Caffrey and Kemp, 1990; Miyajima et al., 2001), but this is not always the case (Boon et al., 1986b). However, reported denitrification rates in seagrass sediments are highly variable (Caffrey and Kemp, 1990; Morell and Corredo, 1993; Blackburn et al., 1994; Rysgaard et al., 1996; Shieh and Yang, 1997; Welsh et al., 2000; species concerned: *Syringodium* sp., *Halodule* sp., and *Thalassia* sp., *Thalassia hemprichii*, *Halodule beaudettei*, *Halodule uninervis*, *Zostera marina*, *Zostera noltii*), with values ranging, generally, from 0.4 to 6 μmol N m^{-2} h^{-1}, but up to 8–30 μmol N m^{-2} h^{-1}, in eutrophicated lagoons with *Zostera capricorni* (Eyre and Ferguson, 2002) and even to 150 μmol N m^{-2} h^{-1} in some cases (Hemminga and Duarte, 2000). Such rates are, on average, lower than those found in coastal sediments without seagrass cover, where nitrogen efflux is in the range 50–250 μmol N m^{-2} h^{-1} (Seitzinger, 1988; Kim et al., 1997; Valiela and Cole, 2002).

Estimation of denitrification rates faces several problems, among which the choice of the methodology (acetylene-block vs. isotope pairing techniques, see Middleburg et al., 1996, Welsh et al., 2001), and the variability (in space and time) of the processes involved, making it difficult to produce accurate annual estimates. This has to be considered when interpreting results, or when attempting comparisons. However, controls on denitrification are probably much more complex in seagrass sediments than elsewhere. Here, nitrate will most certainly be the limiting resource for denitrification, and nitrate supply will be determined by two factors: ammonium availability and nitrification, which in turn will depend on oxygen concentration. Competition for pore water ammonium among bacteria, microalgae, and seagrass roots (Welsh et al., 2000) can limit ammonium supply. Moreover, it is known that oxygen release from roots strongly varies among species and seasons. Finally, a part (sometimes substantial, Caffrey and Kemp, 1990) of the nitrate being reduced ends as ammonium, instead of as N_2. In any case, it would seem reasonable to hypothesize that high denitrification will only occur where (and when) ammonification exceeds ammonium primary producers' demand and where (and when) oxygen efflux from roots can sustain a significant nitrifying activity.

It is clear that the role of denitrification in seagrass beds needs to be further elucidated in the near future. Tentatively, and compared to other important N fluxes reviewed in this chapter (export, storage in the sediment, etc), it would seem that, in general terms, the relative importance of denitrification in the N budget of seagrass beds is from modest to moderate. However, much caution should be applied in this respect.

3. Phosphorus

A large amount of P occurs in inorganic form (Jensen et al., 1998). This inorganic P can be found in two forms: bound to oxidized Fe and bound to Ca. In turn, Ca-bound P can be chemisorbed to $CaCO_3$ or in the form of apatites. Fe-bound phosphorus is often called exchangeable P, as it can redissolve following chemical changes (e.g. decrease in redox potential and increase in acidity) in the sediment, while P is almost irreversibly bound to Ca when apatites have been formed. Some dissolution of the carbonate matrix takes place in the root layer (Jensen et al., 1998).

In general terms, Ca-bound P dominates in carbonate sediments, while Fe-bound P dominates in terrigenous sediments (Koch et al., 2001), and this explains the differences in P availability between these two sediment types, which are discussed below (next section). Although this summary is an oversimplification of the very complex P geochemistry in marine sediments, it can help as a basic view (see also Marbà et al., Chapter 6). Much remains to be investigated in this respect, and, specially, the net rates of P sequestration in seagrass beds.

4. Refractory Material

While there has been intense study of the refractory biomacromolecules in terrestrial and freshwater environments (e.g. Derenne and Largeau, 2001), in seagrass sediments this aspect has received little attention. Moreover, what little information there is refers to carbon fractions and not to nutrients associated to refractory particulate or dissolved organic matter. There is evidence on the abundance of refractory compounds in seagrass sediments (*Posidonia oceanica*, Danovaro, 1996), and the quantitatively most important is probably lignin. Nevertheless, these compounds, formed by long chains of phenolic compounds, are basically a carbon sink as no nutrients, apart from C, are linked to them. However, both N and P appear (or are likely to appear) bound to refractory organic compounds. In effect, available data indicate that organic pools represent a substantial part of sediment P (>50% in Florida Bay, Koch et al., 2001), and most of it is probably in refractory forms. Concerning N, it has been found recently that nitrogen from intrinsically labile amino acids can be preserved in the sediments of continental margins over thousands of years in refractory networks of peptide-like material (Grutters et al., 2002). Since one-third of all the amino acids found in sediments could be directly derived from bacterial cell walls, given the relatively high bacterial activity observed in seagrass sediments (López et al., 1995; Danovaro, 1996), it is reasonable to think that this could be a relevant mechanism for nitrogen immobilization in seagrass sediments.

Factors controlling the burial rate of nutrients in these refractory pools are far from understood; species-specific differences in biochemical composition, oxygen availability, bacterial activity (that can be in turn nutrient-limited), origin of the material (since part can be allochthonous, i.e. of terrestrial origin, or from nearby ecosystems such as mangroves), and temperature are just some of the potential controls to be considered (Henrichs, 1993; López et al., 1995; Mateo and Romero, 1997; Danovaro et al., 2002; Mateo et al., Chapter 7). A very peculiar case of burial occurs when the seagrass belowground organs are stored with no or only slight decomposition, and accumulate as peat-like deposits. This fact has been reported only for a very small number of seagrass species. Such species are, as far as we are aware, *Thalassodendron ciliatum* (Lipkin, 1979), *Posidonia australis* (Shepherd and Sprigg, 1976), and *Posidonia oceanica* (Boudouresque et al., 1980; Romero et al., 1994; Mateo et al., 1997). Only for this last species has the magnitude and dynamics of the deposits been studied, and key aspects concerning their importance for carbon are summarized elsewhere in this book (Mateo et al., Chapter 7). The buried dead materials (rhizomes, leaf sheaths, and roots) of *P. oceanica* have a nutrient content of 20–50% N and 5–20% P, compared with the original living material. This decrease in nutrient concentration takes place very quickly (3–5 yr, Romero et al., 1992). No further changes seem to occur, since the N and P concentration in material 10–20 yr old does not differ from that found in material more than 1,000 yr old. Since bulk decay rates of this detritus have been estimated to be extremely low, between 0.00008 and 0.00036 yr^{-1} (Mateo et al., 1997), it is concluded that nutrient release from it is very low, and that these deposits are long-term nutrient sinks, representing net losses of 0.8 and 0.044 g of N and P $\text{m}^{-2}\ \text{yr}^{-1}$, or, roughly, 7% and 5% of the total plant N and P, respectively, annual requirements for plant growth.

Future efforts in the study of the burial of seagrass production should be devoted to the characterization of the refractory organic matter in general but, more specifically to those compounds containing nitrogen and phosphorus. Nevertheless, the general conclusion so far is that the amount of nutrients lost in terms of burial is modest in terms of the ecosystem budget. However, the role of seagrass beds as nutrient sinks should not be disregarded, especially in the context of coastal waters facing problems of eutrophication (see Marbà et al., Chapter 6).

F. New and Recycled Production in Seagrasses

In general terms nutrient budgets of seagrass ecosystem include an exchange term and a recycling term. That is, the total need of nutrients required for seagrass (and other primary producers within the seagrass bed) growth is met by nutrients coming from outside the system ('new nutrients') or recycled within the system, where the boundaries of the system are defined by the limits of the seagrass distribution, and include some portion of the water column and the upper layers of the sediment. The nutrients can be imported through diffusion or advection, through sedimentation (including filter feeder activity) or, more rarely, through nitrogen fixation. Recycling includes metabolic recycling (nutrient recovery, storage, etc.) and ecosystem recycling (leaching and *in situ* organic matter mineralization, either in the water column, in the sediment surface, or within the sediment). Under the assumption of steady state (that may not necessarily be met), import of new nutrient should equal nutrient losses: burial, export, and, eventually, denitrification. Paralleling classic concepts in plankton ecology (e.g. Dugdale and Goering, 1967; Eppley and Peterson, 1979), it could be said that the relation of the exchange component to the recycled material (or to total, to formally adapt to the f-ratio used in planktonic systems) provides a rough measure of the dependence of the bed on external nutrient sources. Knowledge of how this dependence varies geographically, depending on the water nutrient status or across seagrass species in various ecosystems would be very valuable but has never been attempted, to our knowledge. Yet is has to be acknowledged that the determination of f-ratio in seagrasses poses serious methodological problems, that could be circumvented in the future using stable isotope tracers (see Mateo et al., Chapter 7). In any case, an ecosystem approach to the interactions between nutrients and seagrasses, although difficult, would be desirable to better address key issues, for example those related to seagrass conservation or the biogeochemistry of coastal waters.

IV. Nutrient Limitation and Nutrient Imbalances

A. An Old and Frequently Tested Paradigm

The luxuriant growth, the impressive biomass, and the large areas covered by seagrasses, especially in oligotrophic waters, suggest a very high-nutrient demand to sustain such growth, and point to a possible nutrient limitation. To grow successfully, these plants need physical space (substrate), solar radiation, water, inorganic carbon, and sufficient amounts of all the macronutrients and micronutrients. Among potential limiting factors, and at least in shallow waters, nutrients are the top candidates to be actual limiting resources (see, however, the role of carbon, Larkum et al., Chapter 14).

Thus, it is by no means surprising that the hypothesis of nutrient limitation has been repeatedly addressed, generally using one of the three following approaches: (i) correlational, through the study of plants along nutrient availability gradients, (ii) observational, through the analysis of nutrient concentration and/or proportions in plant tissues, (iii) experimental, through manipulations of natural nutrient concentrations (at least from the early work of Orth, 1977). All three approaches have their weaknesses and their strengths. While it is obvious that the experimental approach is the most robust, it is limited in: space (because a reduced number of plots at a reduced number of sites are studied), time (usually experimental fertilization is done during a short time, typically a year or less), and scope (fertilization mostly affects the plants, but hardly, for reasons of scale, the whole ecosystem). These shortcomings can be circumvented by increasing the field work effort (Fourqurean et al., 1995) or, more economically, by using the two other approaches.

Following Udy and Dennison (1997a), as modified by Touchette and Burkholder, (2000), the response of seagrass to increased nutrient availability fall into four categories: (i) positive response of growth and physiology to the additions in low-nutrient habitats where nutrients are the only environmental factor limiting growth, (ii) positive physiological response but no increase in growth, in low-nutrient habitats where environmental factors other than the added nutrient limit growth, (iii) neither a growth nor a physiological response in high-nutrient environments where nutrient supplies are in excess, and (iv) negative physiological response and inhibition of growth by an added nutrient. The fourth kind of response seems to be the least frequent (but see Burkholder et al., 1992, 1994) and indicates an upper limit for physiological tolerance to nutrients (mostly, nitrate and ammonium).

Concerning responses (i) and (ii), seagrass has been repeatedly observed to positively react to nutrient addition in several nutrient-poor ecosystems around the world (see references in the following section).

The first attempt to make a general hypothesis or prediction about seagrass response to increased nutrient availability was done by Short (1987), demonstrating that seagrasses growing in terrigenous sediment were nitrogen-limited, due to the generally high denitrification rates found in these environments (but see Section III E in this chapter), while seagrasses growing in biogenic carbonate sediments were often phosphorus-limited due to binding of phosphate in the carbonate sediments (Short et al., 1990; Fourqurean et al., 1992), and nitrogen is readily available, e.g. in many tropical ecosystems, through nitrogen fixation. This hypothesis is attractive, since it links seagrass features to the general biogeochemical cycle of nutrients (see preceding sections in this chapter, and Marbà et al., Chapter 6). However, nitrogen limitation of seagrass growth has also been demonstrated in carbonate sediments (Udy et al., 1999), P limitation has been evidenced in sediments with less than 30% of carbonate content (Pérez et al., 1991), and phosphorus deficiency was not found to be linked to carbonate sediment content, at least across a relatively limited geographical area (Invers et al., 1995). These findings indicate that, besides the general nutrient cycle, nutrient limitation in seagrasses is strongly dependent on, at least, specific plant features and local conditions.

Nevertheless, absence of response to nutrient additions is also frequent, even in oligotrophic waters. It has been considered sometimes as an 'experimental failure' and even not worthy of publication (but see Erftemeijer et al., 1994; Romero et al., 1998; Worm and Reusch, 2000, among others). However, if nutrient addition has been performed adequately, such a negative result indicates that nutrient availability is in excess of seagrass nutrient demands. Of course, any explanation based on a sufficiency of nutrient supply must take into account that several of the non-responding seagrasses were growing in oligotrophic waters, bearing in mind the following two observations. First, it has to be acknowledged that seagrasses seem to be adapted for growing in nutrient-poor environments. Not only the mechanisms described in the firsts sections of this chapter (nutrient resorption, use of pore water nutrients, storage, etc.) allows these plants to better use nutrients, but also it has to be considered that seagrasses require approximately 8–50 times less nitrogen and 1.5–100 times less phosphorus for daily growth than macroalgae or phytoplankton, respectively (Duarte, 1995). Second it has to be taken into account that nutrient additions not only modify the plant nutrient availability, but also the ecosystem interaction network, in a kind of cascading of hierarchical effects that can mask the direct, first order effects on plant growth. This aspect, which seems crucial for the understanding of nutrient–ecosystem interactions, will be explored in the next section.

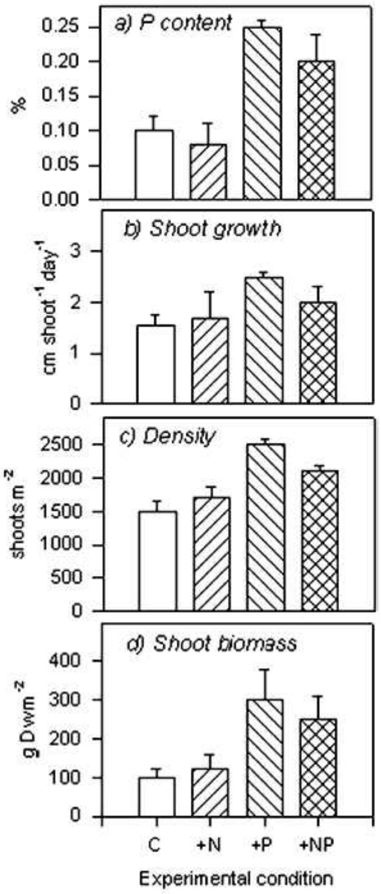

Fig. 4. Sequence of events following nutrient additions in a P-limited seagrass (*Cymodocea nodosa*) bed. In P-treated plots, increased P uptake and assimilation leads to higher P content in leaf tissues (a); this stimulates shoot growth (b) and rhizome branching, which in turn causes a clear shoot density increase (c), the whole resulting in a ca. three-fold leaf biomass increase (d). Redrawn from data in Pérez et al. (1991) and unpublished data.

B. Hierarchical Effects of Nutrients Increases

The increase in nutrient concentrations, either in the water column or in the sediment pore water, initiates a sequence of events that begins with the increase in plant uptake and can be followed by higher nutrient assimilation rates and by other effects in the plant itself (Fig. 4). Other species of the community can be directly (epiphytes, bacteria, etc.) or indirectly (grazers, suspension-feeders, etc.) affected, at their own individual or population levels. Finally, the interaction network can be modified, with responses at the community/ecosystem level.

1. Relationship of Ambient Nutrient Concentration and Uptake Rates

The increase in nutrient availability generally increases nutrient acquisition. In the case of nitrogen, both an increase in uptake (Pérez-Lloréns and Niell, 1995; Pedersen et al., 1997) and in assimilation (i.e. glutamine synthase or nitrate reductase activity, Touchette, 1999) have been reported, and the same is true for phosphorus (Penhale and Thayer, 1980; Pellikaan and Nienhuis, 1988; Pérez-Lloréns and Niell, 1995).

This increased nutrient acquisition is reflected by increases in N and P nutrient content (Duarte, 1990; Bulthuis et al., 1992; Erftemeijer et al., 1994; Alcoverro et al., 1997; Udy and Dennison, 1997a; Lee and Dunton, 1999a; Terrados et al., 1999), and by the increase in the tissue content of glutamine and asparagine (Udy and Dennison, 1997a,b; Udy et al., 1999). It has also been shown that plants exposed to higher N concentrations had higher $\delta^{15}N$ values in their tissues. However, this shift seems to be caused by the higher $\delta^{15}N$ value of the inorganic nitrogen of anthropogenic origin, more than by changes in physiological discrimination during the process of N acquisition. (Udy and Dennison, 1997b; Yamamuro et al., 2003).

2. Flow-On Metabolic Responses

However, this increased uptake is not without consequences for other components of plant metabolism. For example, the relative importance of roots vs. leaves as major sites for nutrient assimilation can shift (Thursby and Harlin, 1982, 1984). Moreover, nutrient assimilation (especially nitrogen) requires carbon skeletons and energy (Turpin, 1991; Huppe and Turpin, 1994; Touchette, 1999), both of which are supplied by photosynthesis. Therefore, high nitrogen assimilation may require increases in photosynthetic C-fixation (Agawin et al., 1996; Lee and Dunton, 1999a). Yet nutrient additions have been shown to stimulate plant carbon production through physiological changes in the maximum rate of photosynthesis, photosynthetic efficiency, and/or increased chlorophyll concentrations (Agawin et al., 1996; Lee and Dunton, 1999a). Alternatively, the need for carbon skeletons can be met by mobilization of carbohydrate reserves, or by the use of fixed carbon that could have been used to build up such reserves; in point of fact, decrease of carbohydrate reserves following nutrient increases has been repeatedly observed (Delgado et al., 1999; Lee and Dunton, 1999a; Invers et al., 2004) and can eventually compromise future growth (Burkholder et al., 1992) or overwintering (Alcoverro et al., 1999; see Fig. 5).

3. Response of Tissues and Organs

At the individual, macroscopic level, increased leaf growth, production, shoot height, blade length and width, and biomass are the most commonly reported responses to increased nutrients (Orth, 1977; Bulthuis and Woelkerling, 1981; Pérez et al., 1991; Tomasko and Lapointe, 1991; Murray et al., 1992; Agawin et al., 1996; Alcoverro et al., 1997; Udy and Dennison, 1997a; Terrados et al., 1999; Lee and Dunton, 2000). Another individual response is the change in the pattern of within-plant resource allocation. In effect, shoot: root ratio increases with fertility, both following nutrient gradients (Pérez et al., 1994; Lee and Dunton, 2000) and in nutrient additions experiments (Powell et al., 1989; Short et al., 1990; Pérez et al., 1991). This behavior implies that seagrasses allocate more biomass in leaf tissues under high-nutrient availability, but more below-ground biomass under low-nutrient conditions. Plants under sediment nutrient deficient conditions increase biomass allocation to below-ground tissues to expand surface area for nutrient uptake (Gleeson, 1993; Vogt et al., 1993), while they increase carbon allocation to the above-ground tissues as a result of nitrogen addition into sediment (Lee and Dunton, 1999a). Changes in seagrass biomass allocation thus reflect a kind of strategy: when nutrients are abundant, leaves seem to be the ‘preferred’ site for uptake; in contrast, when nutrients are scarce, root uptake is maximized.

4. Influences at the Population Level

Nutrients alter population size and/or structure by direct and indirect effects. Nutrient addition has been shown to increase recruitment (Pérez et al., 1991; Fourqurean et al., 1995) and to increase mortality, probably through enhanced intra-specific

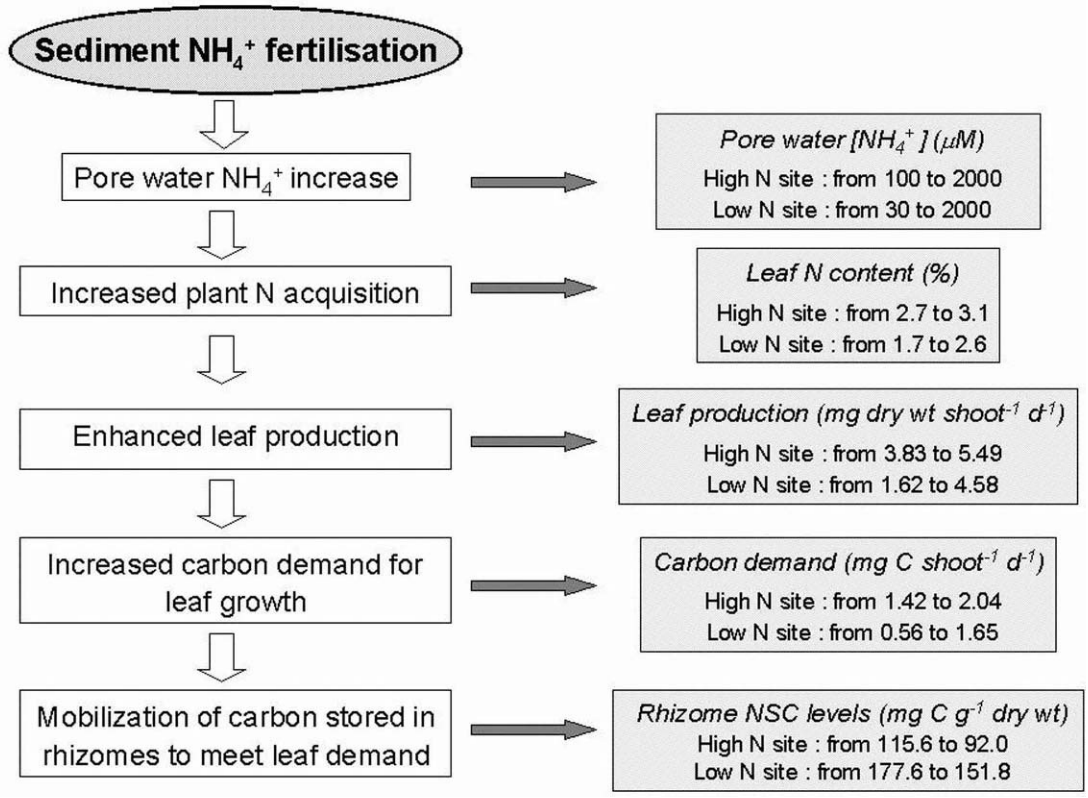

Fig. 5. An example of interaction between N availability and carbon metabolism. The sequence of events driven by nutrient addition (left) results in the decrease of non-structural carbohydrates (NSC) stored in rhizomes. Values and rates for the processes described are given in the right part, indicating the increase after nutrient addition; they are derived from field experiments in two *Thalassia testudinum* stands of contrasting N availability (as in Fig. 1). Redrawn from data in Lee and Dunton (1999a).

competition for light (Pérez et al., 1994). Very little is known on the effects of nutrients on seagrass rhizome architecture. However, the importance of clonal integration observed in seagrasses (Marbà et al., 2002; Duarte et al., Chapter 11) and the rhizome plasticity observed in some species (Terrados et al., 1997a,b) could indicate that nutrients are important factors affecting the branching frequency and angle, and the internode length and, therefore, seagrass colonization rates. This field deserves developing in the future. Finally, at the population level, there are indirect indications of the relation of reproductive output and nutrients. In effect, reproduction also seems to represent a substantial nitrogen investment (Kaldy and Dunton, 2000) and some data suggest that nutrients can also modify allocation of energy and resources to flowering (McMillan, 1980).

At the community/ecosystem level, the diversity of mechanisms and interactions affected by nutrient increase is huge; some have been extensively described, and have become paradigms in coastal ecology, while others remain as promising issues to be explored.

The most frequently invoked change is the reduction in light reaching seagrasses, either due to phytoplankton blooms and to epiphyte overgrowth (Neckles et al., 1993; Coleman and Burkholder, 1995; Moore and Wetzel, 2000). This light attenuation may seriously affect plant viability and cause seagrass decline (Orth and Moore, 1983; Cambridge and McComb, 1984; Walker et al., Chapter 23; but see Borowitzka et al., Chapter 19, Section IV.B.5, below, and elsewhere in this book for the complex interactions of nutrients and epiphytes).

Another classical issue is that concerning the changes in community composition. The replacement of some seagrass species by others caused by nutrient increases takes place only in areas with a relatively rich seagrass flora; generally, early-successional species replace late-successional ones, because the later usually present low growth rates and nutrient demands (Williams, 1987; Fourqurean et al., 1995). Competition between seagrasses and macroalgae (other than epiphytes) can also be modulated by nutrients; in effect, it was observed in a mixed bed of the native seagrass *Cymodocea nodosa* and the introduced alga *Caulerpa taxifolia* that nutrient additions enhanced *C. taxifolia* growth on the short term, but this did not lead to the exclusion of the seagrass, since coexistence was reached in the long term (Ceccherelli and Cinelli, 1997; Ceccherelli and Sechi, 2002).

5. Interaction Networks

Other modifications of the interaction network have been less explored. One of the ecosystem components susceptible to nutrient additions is the bacterial flora, which is of major importance but has received only marginal attention. For example, sediment nutrient enrichment in oligotrophic waters can stimulate bacterial growth and activity, with bacteria competing for nutrients with seagrass roots (López et al., 1998) and eventually induce oxygen depletion in the pore water. Phosphorus addition can be beneficial for N-fixating prokaryotes, potentially confounding the results of fertilization experiments (Powell et al., 1989). The role of bacteria in the nutrient cycling in seagrass beds has been studied, but much more needs to be elucidated in order to yield an understanding of the controls on bacterial activity.

Another aspect of the interaction network modified by nutrient availability concerns the interplay among epiphytes, herbivores, and the plant itself. In a relatively large area affected by nutrient increase, the standing crop of seagrass was clearly declining, and a die-off of the bed was observed, due to a large increase in the herbivore population and in herbivore activity (Ruiz et al., 2001). The reason for this is unclear, but it can be hypothesized that carbon skeletons were diverted from secondary metabolism to growth as nutrient availability increased, causing a decrease in chemical deterrents. An alternative (or complementary) explanation is that the increase of N in leaves made them more palatable to herbivores. Similar findings were reported in McGlathery (1995). Hence, nutrients would have to shift the control of seagrass abundance from resources (bottom-up) to predators (top-down). However, herbivore–plant interaction is more complex, since it is, at least in part, mediated by epiphytes, and herbivores may be more attracted by algal epiphytes than by seagrass leaves (Kitting et al., 1984). However, epiphytes are also strongly affected (both in quality and in quantity) by nutrients, and in turn can reduce light reaching the leaf surface. Therefore, it is also possible to find positive effect of herbivores under high-nutrient availability, by reducing epiphyte biomass (Heck et al., 2000).

In short, it is clear that a complete understanding of the consequences of nutrient enrichment for seagrass ecosystems has not yet been fully achieved, and while physiological and other individual processes are relatively well known, some of the responses at the ecosystem level still need to be elucidated, mostly those linked to biotic interactions. Yet it is clear that this is a key point in seagrass ecology, as an issue of basic knowledge but also as a tool to predict, mitigate, and/or manage the impacts of anthropogenic eutrophication (see Ralph et al., Chapter 24).

V. Conclusion and Future Goals

Nutrient fluxes are essential components of the material and energy flow that sustains ecosystems. Nutrient–seagrass interactions can be viewed under, at least, three perspectives: (i) nutrient dynamics in seagrass beds (how nutrients enter, how they are used and recycled, and how they leave these ecosystems), (ii) influences of nutrient abundance on seagrass beds (how changes in nutrient supply alter functional aspects of the plant and modify ecological interactions), and (iii) influence of seagrass beds on nutrient cycles (how seagrasses modify the general nutrient fluxes in coastal waters). This chapter has focused mainly on the first two, and it is clear that a good understanding of them requires a multilevel approach, encompassing perspectives ranging from physiological, and even molecular, to ecological, and even biogeochemical. The effects of nutrient additions provide a good example of this hierarchical nature of seagrass–nutrient interactions, which includes from changes in physiology to changes in the community interaction network.

A large body of work has been done in this field, which is, certainly, a favorite topic in seagrass biology. In this chapter, which was not aimed at providing a thorough and exhaustive literature review, around 150 references (strictly concerning seagrasses) have been cited, evidence in itself of a sustained research effort. Although this research effort has allowed a progressive understanding of the different issues expressed above, large gaps, concerning almost any of the subjects addressed (e.g. within-plant transport mechanisms, microbial processes in the sediment, organic and inorganic nutrient accumulation, etc.) are evident, and it is clear that sustained effort is still needed to fill these gaps. It has also to be acknowledged that despite the work done by seagrass biologists, we are at least a step behind what is known concerning nutrient–plant interactions in terrestrial ecosystems. The latter is a great source of new ideas and techniques. It is rather difficult to foresee the best direction for fruitful research in the coming years. Most probably, several approaches will produce significant advances. However, one has the impression that the most exciting endeavor in this field would be the attempt of a large, ecosystem-level, experiment in which multidisciplinary teams would address different aspects of seagrass–nutrient interaction from the three perspectives listed above. This is more a dream than a guess. In any case, basic research should aim to explore the less known aspects identified in this chapter (and, desirably, also others). Moreover, there is an increasing demand for knowledge to be applied to seagrass conservation (see Kenworthy et al., Chapter 25). Since anthropogenic eutrophication is one of the main threats to seagrass ecosystems, providing society with this knowledge falls within the scope of the topic of this chapter; and is a basic duty of the scientific community.

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Chapter 10

Oxygen Movement in Seagrasses

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I. General Introduction

Seagrasses are, like all vascular plants, obligate aerobes, which require a continuous supply of oxygen to sustain aerobic metabolism of both above- and below-ground tissues. Compared to their leaves, seagrass roots and rhizomes may experience oxygen deprivation for shorter periods, but these below-ground tissues exhibit physiological adaptations which allow them to rely temporarily on anaerobic fermentative metabolism (Pregnall et al., 1984; Smith et al., 1988). Aerobic respiration is energetically about 10 times more efficient than fermentative processes, which tend to accumulate ethanol, acetate, and other potentially toxic metabolites representing a threat to tissue survival (Smith et al., 1988; Crawford and Braendle, 1996). The meristematic tissues, located in the transition between water column and sediment, are especially vulnerable to low oxygen supply and exposure to anaerobic metabolites due to their high metabolic activity and the continuous oxygen supply required for mitotic growth. In addition to the importance of oxygen inside seagrass tissues, maintenance of oxic conditions around roots may provide efficient protection against invasion of reduced toxic compounds and metal ions from the surrounding sediment (Armstrong et al., 1992; Crawford and Braendle, 1996; see also Marbá et al., Chapter 6). Accordingly, there are several benefits to plant performance in maintaining a rich oxygen supply to all tissues including roots and rhizomes.

In most terrestrial plants oxygen is readily supplied from the atmosphere and from aerated soils. However, emergent wetland plants rooted in waterlogged soils or submerged macrophytes, such as seagrasses, must temporarily or permanently endure conditions with low supplies of oxygen from the surrounding environment. Coastal marine sediments are mostly anoxic and highly reduced because of the degradation of organic matter within the sediment and slow oxygen diffusion from the water column. Hence the sediment represents a strong oxygen sink rather than a source, and oxygen must be supplied to below-ground tissues of seagrasses either by photosynthesis or by oxygen diffusing from the water column through leaves to rhizomes and roots (Pedersen et al., 1998). The slow diffusion of oxygen in water (10,000 times slower than in air) contributes to the potential risk of oxygen deprivation in submerged plants. Firstly, transport of oxygen from the water column through the relatively thick diffusive boundary layers around leaves is impaired by the slow rate of diffusion, and secondly, liquid phase oxygen diffusion inside plants is grossly inadequate to support oxygen transport over long distances such as those between leaves and root tips. Therefore, submerged plants have become anatomically adapted to oxygen shortage by developing aerenchymatic tissues with continuous air-filled lacunae running from leaves to roots (Armstrong, 1979; Larkum et al., 1989; Kuo and den Hartog, Chapter 3).

This chapter aims to present the current status of knowledge with respect to oxygen production, consumption and transport within seagrasses. We

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describe and evaluate the techniques, which have been used for estimating or directly measuring oxygen variability and transport in seagrasses. Next, we address the internal and external sources of oxygen, sinks of oxygen and transport of oxygen between tissues. We demonstrate the factors controlling internal oxygen variability by means of manipulations under controlled conditions in the laboratory and present data on *in situ* oxygen variability from seagrass stands. Finally, we briefly discuss the potential coupling between seagrass oxygen dynamics and the occurrence of die-off events in seagrass beds.

II. Measuring Oxygen Dynamics and Transport

A. Difficulties in Measuring Oxygen Dynamics and Transport

Measuring oxygen production, consumption, release and transport in seagrasses and other rooted macrophytes is a major technological challenge. A number of different techniques are available and have been applied, but all methods seem to have potential drawbacks depending on the specific objective. The intrinsic problems are related to the fact that all rates of oxygen exchange within plants depend on a complex of factors such as (1) the immediate size of oxygen pools within specific plant tissues and in the media surrounding leaves and roots, (2) the resistance to transport within plants and between plant and media, and (3) the steepness of gradients within tissues and between tissues and the surrounding media. The factors vary temporally and spatially under natural conditions and these changes are difficult to control and mimic in the laboratory. Assessment of oxygen dynamics within and around seagrasses under controlled laboratory conditions is, therefore, best suited for describing relative rates and mechanisms rather than determining absolute rates as they would occur under natural conditions.

B. Chamber Techniques

Oxygen release and consumption have traditionally been assessed by measuring changes in bulk water oxygen concentrations in incubation chambers. This technique is feasible for measurements of photosynthesis and respiration of isolated leaves, although potential problems with lacunar oxygen accumulation, and especially with poor simulation of natural boundary layer conditions around leaves, may interfere significantly with rate measurements. Measurements of respiration in isolated roots and rhizomes using chamber techniques can be more problematic. It has been argued that measuring respiration of isolated below-ground tissues under aerobic conditions may overestimate the respiration that would occur in anoxic sediments (e.g. Smith et al., 1988; Touchette and Burkholder, 2000). However, such a procedure may also underestimate respiration, because the lacunar oxygen supply from leaves to roots and rhizomes is disrupted when the tissues are separated from the leaves. Hence, respiration has to be fueled by oxygen diffusing from the bulk water through boundary layers and through the more or less permeable root and rhizome tissues, and this diffusion may be too slow to sustain an adequate internal oxygen supply and mimic natural conditions of intact plant gas phase transport (Saglio et al., 1984).

Chamber techniques provide reliable estimates of whole plant metabolism if intact plants with leaves, roots and rhizomes are incubated for longer time intervals allowing equilibration of oxygen between lacunae and bulk water (Kemp et al., 1986). In addition, split chambers with leaf compartments separated from root compartments by water- and gas-tight seals have been used to estimate oxygen transport from leaves to roots and subsequent oxygen release to the sediments (e.g. Sand-Jensen et al., 1982; Kemp and Murray, 1986). Results based on this technique have, however, to be interpreted with caution. Transport from leaves to roots is driven by gradients between sources and sinks, and the steepness of these gradients depend greatly on the experimental conditions (Sorrell and Armstrong, 1994). The oxygen gradient from the root to the sediment is especially important, because it determines the rate of oxygen loss to the sediment and because it can vary by an order of magnitude depending on the oxygen consumption within the root medium (Sorrell and Armstrong, 1994). To mimic natural sediments as proper sinks the rooting media must not only be anoxic but also reducing and oxygen consuming to generate the sufficiently steep gradients between root and sediment forcing the release of oxygen. Such conditions can be established by

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Abbreviations
DBL – diffusive boundary layer
KPa – kilo Pascals
Rubisco – Ribulose-1,5-bisphosphate carboxylase-oxygenase.

adding titanium citrate buffer to the root medium thereby increasing measured rates of oxygen release from the roots (Sorrell and Armstrong, 1994). However, if simulating natural conditions properly the split chamber techniques provide the most reliable estimates of whole plant oxygen transport.

C. Gas Extraction Techniques

Changes in internal pools of oxygen in plants may be more directly assessed by extracting oxygen from the lacunar spaces of different tissues (e.g. Oremland and Taylor, 1976; Carlson et al., 1988). This technique is usually destructive in the sense that tissues have to be cut or squeezed to harvest internal gases, but the method does allow assessment of diel changes in lacunar oxygen and, in addition, extracted air-samples can be analyzed for concentrations of internal CO_2, N_2 and CH_4 using infrared gas analysis and gas chromatography at high precision (Hartman and Brown, 1967; Oremland and Taylor, 1976; Larkum et al., 1989). However, the gas extraction technique does not allow on-line recording of internal gas dynamics as functions of changes in environmental conditions and the technique has poor temporal and spatial resolution.

D. Microtechniques

Microelectrodes, compared to other techniques, do provide much more elegant opportunities for online assessment of internal oxygen conditions within plants (e.g. Armstrong et al., 1994; Armstrong et al., 2000; Greve et al., 2003). Some of the earliest microelectrodes for measuring internal oxygen contents in plant tissues were polarographic electrodes requiring external reference electrodes, and therefore oxygen could only be assessed in the liquid phase and not in air-filled lacunae (e.g. Bowling, 1973). The appearance of fast-responding and stirring-independent Clark-type oxygen microelectrodes with built-in guard cathodes provided the first means of microscale oxygen measurements in both liquid and gas phase at high spatial and temporal resolutions (Revsbech, 1989). The technique allows measurements of internal plant gradients and oxygen profiles on root surfaces at spatial scales of 10 μm or less (Caffrey and Kemp, 1991; Armstrong et al., 1994; Christensen et al., 1994; Pedersen et al., 1998; Greve et al., 2003) and at temporal scales of less than 1 s. Hence, rates of oxygen release or consumption can be continuously and precisely assessed in specific tissues under natural or manipulated conditions. The high spatial resolution, however, has the drawback that the overview of whole plant metabolism or oxygen release is lost. Such processes are better determined by using chamber techniques under proper mimicry of natural conditions.

Microoptodes also provide means of measuring oxygen and other compounds at high spatial and temporal resolution, and, in addition, the optode technique has been developed to allow two dimensional recording of changes in oxygen conditions in sediments, microbial mats and in the rhizosphere of aquatic plants (Glud et al., 1996). The planar optodes, potentially, provide excellent means for assessing spatial differences in oxygen concentrations around roots and rhizomes of intact plants as a function of experimentally altered conditions for plant photosynthesis.

III. Oxygen Sources

The supply of oxygen to support aerobic metabolism within seagrass tissues derives from internal oxygen produced by photosynthesis and from passive diffusion of oxygen from water column or sediment, when oxygen partial pressures in the external media surpass plant oxygen partial pressures (Fig. 1). Photosynthesis of seagrasses mainly takes place in the epidermal cells with high chlorophyll contents assumed to represent an adaptation to the low light conditions often experienced by submerged macrophytes (Kuo and McComb, 1989; Larkum et al., 1989). Rates of photosynthesis on a dry weight basis are relatively low for seagrasses and other hydrophytes compared to terrestrial plants (Bowes, 1985; Nielsen and Sand-Jensen, 1989; Larkum et al., Chapter 14). However, high rates of oxygen evolution take place in individual leaves which is immediately apparent as formation of numerous gas bubbles during calm, sunny days (Zieman, 1974). In addition, leaf biomass of some seagrass beds may be very high and gross primary production can exceed 10 g O_2 m^{-2} d^{-1} (Ziegler and Benner, 1998; Hemminga and Duarte, 2000).

A. Oxygen Evolution by Photosynthesis

Gross photosynthesis of seagrass leaves exceeds respiratory demands by almost an order of magnitude

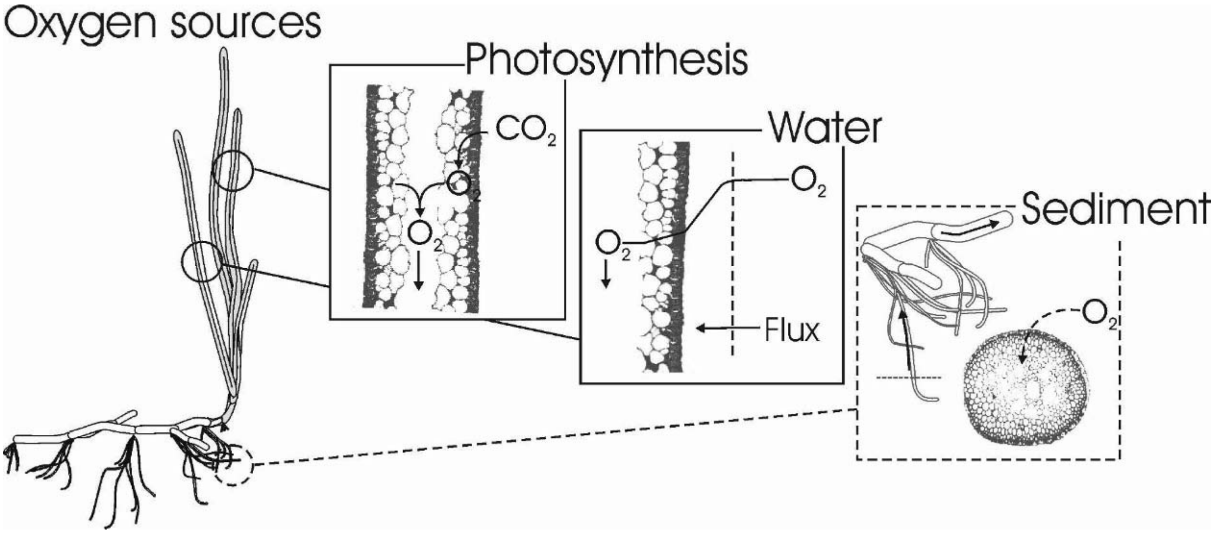

Fig. 1. Schematic representation of the potential sources of oxygen in seagrasses. In the light, photosynthetic oxygen evolution in the leaves is the only source of plant oxygen. In darkness, when internal leaf oxygen partial pressure declines below that of the water column, oxygen is supplied to leaves by passive diffusion from the water. Theoretically, the sediment could be a source of oxygen, if partial pressures in the sediment exceeded those of roots and rhizomes, but the rhizosphere of seagrasses is usually anoxic.

(Touchette and Burkholder, 2000; Larkum et al., Chapter 14) and generates a considerable internal build-up of oxygen pools inside the tissues and in leaf lacunae. Extracted gas samples from seagrass leaves have contained oxygen of 30–35 kPa equal to 10–15 kPa above air saturation (Oremland and Taylor, 1976; Roberts and Moriarty, 1987; Larkum et al., 1989) and up to 55 kPa in other submerged macrophytes (Hartman and Brown, 1967). Microelectrode techniques, similarly, have recorded high internal oxygen partial pressures in seagrasses (Greve et al., 2003; Borum et al., in preparation). The oxygen partial pressure inside the meristematic region of *Zostera marina* and *Thalassia testudinum* can increase from virtually zero, reached during prolonged darkness, to more than 40 kPa within 60–120 min at saturating irradiances. These high internal oxygen partial pressures in part result from the increased proportion of oxygen in the lacunal gas and in part by the overall increase in gas pressure inside leaf lacunae.

High internal oxygen partial pressure may by itself affect seagrass photosynthesis by generating photorespiration due to the competition between oxygen and carbon dioxide for binding sites in Rubisco (Søndergaard and Wetzel, 1980; Touchette and Burkholder, 2000; Larkum et al., Chapter 14). In the submerged macrophyte *Scirpus subterminalis* photorespiration increased from about 10% of net photosynthesis at normal external oxygen partial pressures to 30% at external partial oxygen pressures above 35 kPa (Søndergaard and Wetzel, 1980). The influence of high oxygen contents on photorespiration has, to our knowledge, not been examined for seagrasses.

B. Oxygen Supply from the Surrounding Media

In the absence of photosynthetic oxygen evolution, it has often been assumed that the aerobic metabolism of seagrass tissues must rely on internal pools of oxygen built-up during the day (Smith et al., 1984; Pregnall et al., 1984; Hemminga, 1998). However, oxygen can readily diffuse from the water or sediment into the plant when external oxygen concentrations exceed internal concentrations. Oxic rhizospheres have been reported for rosette plant communities in oligotrophic lakes (Christensen et al., 1994; Pedersen et al., 1995), but usually sediments of rooted macrophyte beds are anoxic and cannot function as a source of oxygen for root metabolism (Armstrong, 1979). However, passive influx of oxygen from the water column has been clearly shown to ensure internal oxygen status of seagrass tissues reflected by sustained oxygen loss from roots to sediment during darkness (Fig. 2; Pedersen et al., 1998), and transport of oxygen from water column to root media in the dark has also been described for submerged

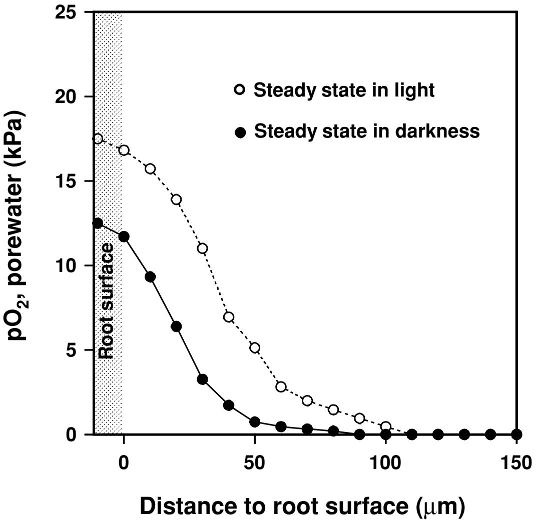

Fig. 2. Steady state microprofiles of oxygen within the sediment vs. distance to the root surface of *Zostera marina* measured in the light (open symbols) and in the dark (solid symbols). Presence of the oxygen profile in the dark, although at a lower level than in the light, documents that oxygen is transported from the water column, as the only possible source in the dark, through the lacunae of leaves to rhizomes and roots, and that this source is sufficiently strong to supply oxygen to the roots in excess of respiratory demands (Pedersen, Borum and Greve, unpublished).

freshwater plants (Sand-Jensen et al, 1982; Sorrell and Dromgoole, 1987).

Rates of passive influx of oxygen from water into leaves can be calculated according to Fick's first law (see section III, Koch et al., Chapter 8). The influx depends on the difference between oxygen partial pressures outside and inside the plant (i.e. the gradient driving the diffusion), the traveling distance across the diffusive boundary layer (DBL) and cuticle/cell wall and the diffusion coefficients of oxygen in water and tissue components (Larkum et al., 1989; Pedersen et al., 1998). Larkum et al. (1989) reported estimates of diffusion coefficients for cuticle and cell walls and estimates of boundary layer thickness around seagrass leaves ranging from 50 to 1000 μm depending on flow regime. Precise measurements of the thickness of boundary layers around leaves are not easily achieved, but again the microelectrode technique provides suitable means for microscale profile descriptions and hence for measurements of boundary layer thickness under standardized conditions. By inserting microelectrodes through the leaf and out into the boundary layer, the extension and dynamics of the DBL can be described without disturbance caused by the electrode tip itself (Glud et al., 1994). Unpublished data from leaves of eelgrass exhibited DBL thickness ranging from 140 to 440 μm at water flow velocities between 11.2 and 0.3 cm s^{-1} (Fig. 3; Peter Larsen, unpublished).

The rates of passive oxygen influx calculated from the data in Fig. 3, and assuming a diffusion coefficient of 2×10^{-9} m^2 s^{-1}, ranged between 0.22 and 0.26 μmol O_2 dm^{-2} min^{-1}. These rates are 10–30% of reported rates of photosynthetic oxygen evolution in eelgrass leaves (Touchette and Burkholder, 2000; Larkum et al., Chapter 14) clearly reflecting the potential importance of passive influx to leaves as a source of oxygen. The calculated rates of oxygen influx are similar and, under the experimental

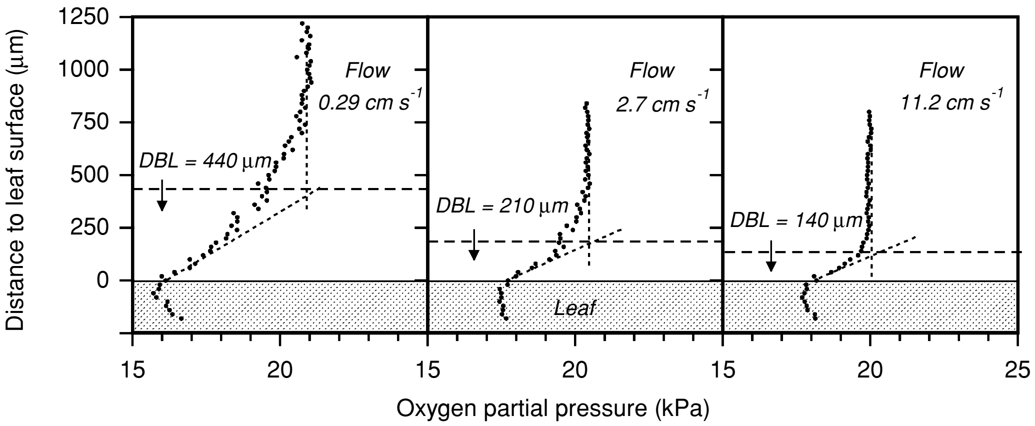

Fig. 3. Oxygen profiles measured by microelectrodes on the surface of eelgrass leaves at different water flow velocities along the leaves. The thickness of the diffusive boundary layer can be determined from the profiles showing reduced thickness with increasing flow velocity (Peter Larsen, unpublished).

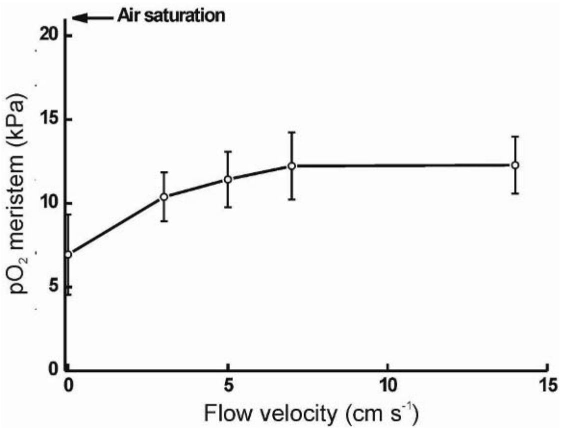

Fig. 4. Oxygen partial pressure in horizontal rhizomes of *Cymodocea nodosa* as a function of water flow velocity around the leaves measured in darkness. Intact shoots were rooted in sediment and exposed to variable flow regimes in the laboratory. Flow velocity was measured ~5 cm above the sediment upstream the plant. Reduced flow results in reduced internal oxygen partial pressure due to the increasing thickness of the diffusive boundary layer around the leaves (Binzer, Borum and Pedersen, unpublished.).

conditions with isolated leaves, represent an estimate of leaf respiration which is independent of the DBL thickness and the lacunal oxygen partial pressure, at least if oxygen partial pressure is not very low.

The overall effect of reduced water flow and increased thickness of the DBL is that the oxygen partial pressure inside plant lacunae declines in the dark (Fig. 4). The influence of reduced water flow on plant oxygen status has been demonstrated for *Cymodocea nodosa* (Fig. 4). Intact shoots with rhizome sections were exposed to different water flow velocities in the dark, and the rhizome internal oxygen partial pressures declined systematically at flow velocities below ~7 cm s^{-1}. Consequently, problems related to low internal oxygen contents in seagrasses may be exacerbated in dense seagrass beds with reduced flow or if flow velocities decline in very calm weather.

The presence of epiphyte communities on submerged plants may further expand the diffusive boundary layer around leaves. The DBL-thickness may increase to several millimeters corresponding to a factor of 5 or more (Sand-Jensen et al., 1985). Therefore, apart from the direct effect of epiphyte activity on oxygen conditions immediately around leaves, the physical presence of the epiphytic community may reduce oxygen influx to less than 20% of that in leaves free of epiphytes. Taking the metabolic activity of the epiphytes into account, consequences for the oxygen balance of leaves and whole plants may be much more pronounced. Sand-Jensen et al. (1985) showed that the oxygen partial pressure in epiphyte communities on leaves of submerged plants could vary from 0 kPa in the dark to more than 45 kPa (i.e. >2 times atmospheric saturation) in the light. Hence, the metabolic activity of dense epiphyte communities may completely disrupt the supply of water column oxygen to leaves during darkness and substantially impede oxygen release from the leaves during periods of high leaf photosynthesis. Epiphyte density on seagrass leaves increases as a function of nutrient richness (Borum, 1985), so eutrophication can severely impair growth conditions of seagrasses by epiphytes creating not only a barrier to light and inorganic carbon but also to oxygen diffusion (Sand-Jensen, 1977; Sand-Jensen et al., 1985).

IV. Oxygen Sinks

Oxygen is lost from seagrasses by respiratory consumption, by release to the water column and by loss of oxygen to the sediment (Fig. 5). In the light, the respiratory oxygen consumption is supported by oxygen produced within the leaves while oxygen is supplied from the water column during darkness (see Fig. 4; Larkum et al., Chapter 14). Oxygen is only lost from leaves to the water column during the day, when the oxygen content within the leaves exceeds concentrations in the water, while oxygen is continuously lost from roots and rhizomes to the sediment both in the light and during darkness.

A. Oxygen Loss by Respiration

Plant respiration represents a significant loss of internal oxygen. While the majority of oxygen is lost by diffusion to the water column and sediment during periods of high net photosynthesis, during periods of low photosynthesis or darkness the major sink for oxygen is respiration. However, it is difficult to estimate the exact loss of oxygen in proportion to the overall oxygen balance of the plants because several loss processes, compartments and driving forces are involved.

Dark respiration of leaves has been determined for several seagrass species (e.g. Larkum et al., 1989; Hemminga and Duarte, 2000; Touchette and

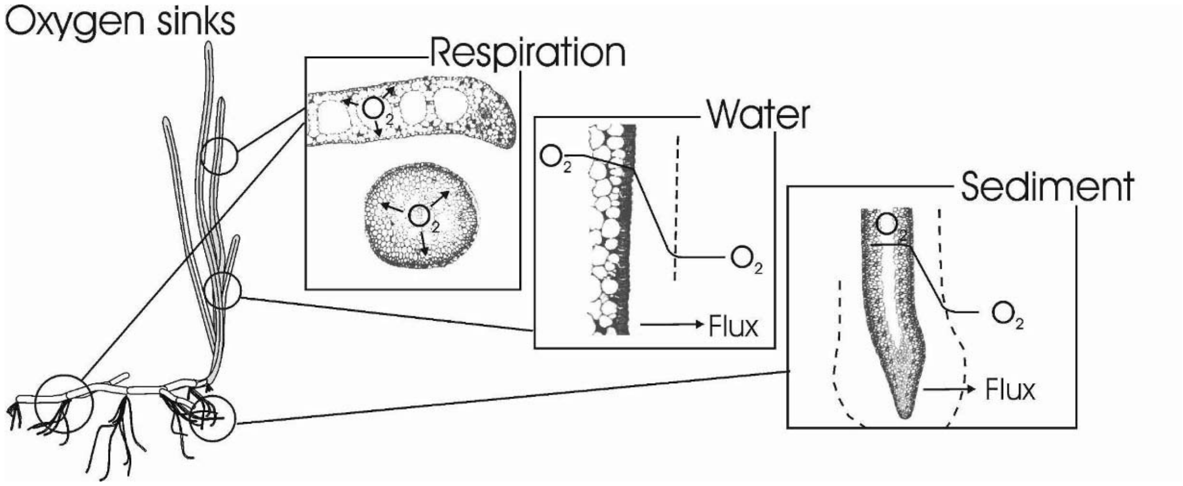

Fig. 5. Schematic representation of the oxygen sinks for seagrasses. Oxygen is continuously lost by respiratory oxygen consumption in leaves, rhizomes, and roots. In the light, oxygen produced by photosynthesis is also lost by bubble formation or by diffusion to the water column. Oxygen is continuously lost from roots and rhizomes to the reducing sediment. Oxygen levels across leaf surface and DBL, in the light, and root surface are graphically represented; dashed lines indicate the limit of the diffusive boundary layer (see text).

Burkholder, 2000; Larkum et al., Chapter 14), and there are no major methodological obstacles in assessing these rates. In eelgrass and other seagrass species leaf respiration ranges from 10 to 30% of maximum photosynthetic rates (Drew, 1979; Caffrey and Kemp, 1991). Weight specific rates of respiration in below-ground tissues are significantly lower than in leaves reflecting lower metabolic activity (Marsh et al., 1986; Caffrey and Kemp, 1991).

The influence of high temperature on rates of respiration constitutes a problem of potentially large importance for the oxygen balance of submerged plants. Respiration seems to increase faster than photosynthesis with increasing temperature (Marsh et al., 1986; Masini et al., 1995; Masini and Manning, 1997) and, in contrast to photosynthesis, which exhibits optimum rates at moderate temperatures, respiration continues to increase up to high temperatures. The effect of increasing respiration above an optimum temperature is, that the oxygen content of the shoots declines dramatically at high temperatures, and plant tissues may turn anoxic even in the light (Greve et al., 2003). At less extreme temperatures, the strength of the respiratory oxygen sink may become so high, that the transport of oxygen to below-ground tissues is insufficient to maintain aerobic respiration and radial oxygen loss to the sediment (Caffrey and Kemp, 1991). This situation represents a threat to plant survival, because toxic anaerobic metabolites (ethanol, lactic acid, etc.) may accumulate within roots and rhizomes (Pregnall et al., 1984; Smith et al., 1984).

B. Oxygen Loss to the Water Column

Oxygen is lost from the leaves to the water column during the day when the oxygen partial pressure within the leaves, produced by photosynthesis, exceeds the oxygen partial pressure of the water column surrounding the leaves. The oxygen may either be lost by passive diffusion through the DBL or by bubble formation on the leaves. Pressurization of fully submerged macrophytes has been described for *Egeria densa* attaining lacunal gas pressures up to 25 kPa above atmospheric pressure (Angelstein, 1910; Sorrell and Dromgoole, 1988). The pressurization can result in bubble formation at leaf tips, but bubbles can also be formed on leaf surfaces as a result of oxygen loss by diffusion across the leaf epidermis. Under calm, warm conditions the release of oxygen into the diffusive boundary layer around leaves may increase local oxygen concentrations above the solubility in water. Bubble formation is, however, less important when the water flow around leaves is high enough to reduce the thickness of the boundary layer and lower the pressurization within the leaves (Sorrell and Dromgoole, 1988).

The relative importance for the overall oxygen balance of seagrasses, of the oxygen lost from leaves to the water column, probably varies substantially with plant morphology (biomass/area of leaves vs.

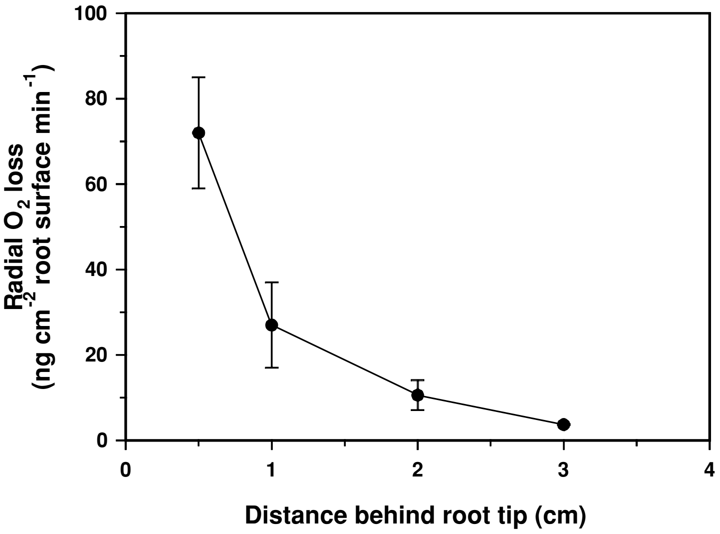

Fig. 6. Radial oxygen loss from roots of *Halophila ovalis* as a function of distance from the root tip ($n = 5 \pm$ SE). Relatively low permeability of older parts of the roots prevents oxygen from being lost to the sediment before reaching the young and actively growing root tips (Redrawn from Connell et al., 1999).

below-ground tissues) and with strength of respiratory sinks within the plants and sediment. Split chamber experiments with *Zostera marina* have suggested that most of the oxygen produced by photosynthesis escapes to the water column (Sand-Jensen et al., 1982; Kemp and Murray, 1986; Caffrey and Kemp, 1991), in agreement with theoretical predictions (Larkum et al., 1989). However, the absolute rates of oxygen loss to the water column may be substantially biased by experimental conditions (Sorrell and Armstrong, 1994) and are highly dependent on plant species and the permeability of leaves (Sand-Jensen et al., 1982).

C. Oxygen Loss to the Rhizosphere

Oxygen loss to the rhizosphere of submerged plants will similarly vary with plant morphology, but a significant loss of oxygen to the sediment from roots of wetland and submerged plants is inevitable (Armstrong et al., 1994). Meristems in root tips must be supplied with sufficient oxygen to support mitosis and efficient energy utilization (Armstrong, 1979; Crawford and Braendle, 1996). To ensure sufficient oxygen supply along the length of roots to the root apex, the radial loss from root surfaces of seagrasses and other aquatic plants seems to decline substantially with increasing distance to root tips (Fig. 6; Armstrong, 1971; Connell et al., 1999; Armstrong et al., 2000; McDonald et al., 2002). However, it is likely that the radial loss of oxygen from root surfaces to the rhizosphere is vital to protect root tissues by oxidizing reduced phytotoxins such as Mn^{2+}, Fe^{2+} and sulfide (Mendelssohn and Postek, 1982; Armstrong et al., 1996; Lee et al., 1999; Marbá et al., Chapter 6, section III.E).

The proportion of oxygen lost to the sediment is difficult to estimate precisely. A comparison of oxygen release from roots of different submerged aquatic macrophytes have documented the high variability among species ranging from about 1% to 100% of total oxygen release in the light (Sand-Jensen et al., 1982). Caffrey and Kemp (1991) found that about 10% of the oxygen produced by photosynthesis in *Z. marina* was released by below-ground tissues, but these estimates could be too low because measurements were conducted with the roots and rhizomes in non-reducing media and therefore with less steep concentration gradients between plants and media than are likely to occur in nature. Also, oxygen release from roots, expressed as a proportion of photosynthetic oxygen evolution, is a rather confusing expression, since it implies that all oxygen released originates from plant photosynthesis, which is not the case. The oxygen released to the sediment in the light is produced by leaf photosynthesis, but oxygen lost to the sediment in darkness originates from the water column.

There is no doubt that the oxygen released from roots to rhizospheres of submerged macrophytes can

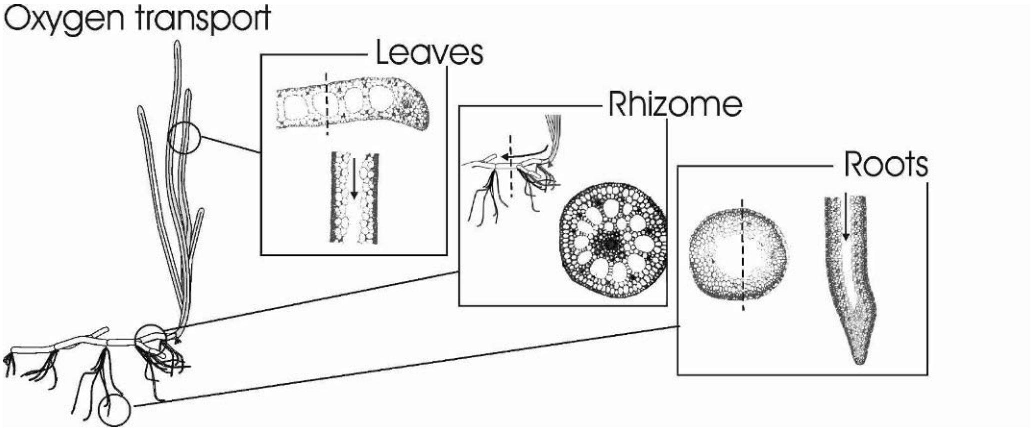

Fig. 7. Schematic representation of the internal transport of oxygen in seagrasses. The transport is basically unidirectional from the high oxygen partial pressures in leaves or surrounding water to the low partial pressures in rhizomes, roots and sediment.

contribute significantly to aerobic mineralization of organic matter within the sediments (Sand-Jensen et al., 1982). For the tropical seagrass, *Cymodocea rotundata*, the estimated amount of oxygen released to the sediment was about the same magnitude as oxygen transported from the water column to surface sediments (Pedersen et al., 1998, 1999). Accordingly, the oxygen loss to sediments has important implications for the degradation of organic matter but potentially also for other redox processes such as sulphide reoxidation (Lee and Dunton, 2000) and coupled nitrification–denitrification (Caffrey and Kemp, 1992). By leaking oxygen from the roots at different rates during light and dark periods, the rhizosphere immediately around roots of aquatic plants experiences fluctuating aerobic and anaerobic conditions which may promote denitrification (Christensen and Sørensen, 1986; Caffrey and Kemp, 1990; Caffrey and Kemp, 1992; Flindt, 1994). However, *in situ* observations of coupled nitrification–denitrification in beds of *Zostera marina* and *Z. noltii* have not demonstrated higher rates than in bare sediments (Rysgaard et al., 1996; Risgaard et al., 1998), so there is a need for more detailed analysis of the complex interactions between plant oxygen release and sediment processes (see also Marbá et al., Chapter 6).

V. Internal Movement of Oxygen

A. General Characteristics

The internal transport of oxygen in seagrasses is predominantly unidirectional from leaves to rhizomes to roots driven by the gradient between high oxygen partial pressures in leaves or water and low partial pressures in roots and sediment (Fig. 7). Seagrasses have well-developed lacunae in leaves, rhizomes and roots with tissue porosities up to 30% or even more (Penhale and Wetzel, 1983; Larkum et al., 1989). The leaf lacunae are connected to the rhizome lacunae (Kuo et al., 1981; Kuo and Den Hartog, Chapter 3); there are often diaphragms at the nodes and transition regions, but these offer little resistance to gaseous diffusion (Larkum et al., 1982). From the rhizome, lacunae continue into each root. Oxygen transport to the most distal, newly formed root tips, however, relies on liquid phase diffusion over short distances (Armstrong, 1979; Colmer, 2003). The formation of air-spaces within below-ground tissues seems to be stimulated by ethylene produced under conditions with low internal oxygen contents (Drew et al., 2000; Colmer, 2003), and lacunal development in eelgrass has been shown to increase with higher sediment organic content and lower redox potential (Penhale and Wetzel, 1983).

B. Oxygen Transport by Diffusion

Gas transport within the majority of emergent and submerged aquatic plants is believed to be driven primarily by diffusion rather than by convective flow (Armstrong, 1979; Sorrell and Dromgoole, 1987; Larkum et al., 1989). Passive gas phase diffusion within seagrasses occurs continuously along the downhill partial pressure gradients from leaves to rhizomes to roots. In the light, the high

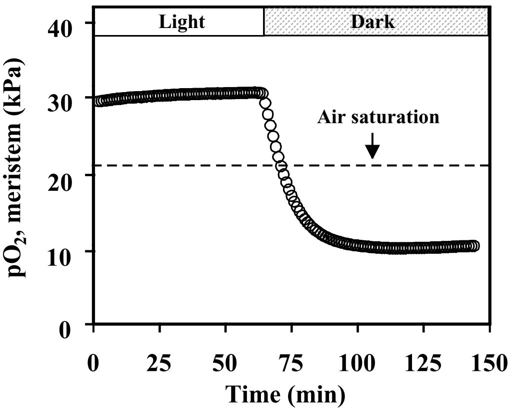

Fig. 8. Changes in oxygen partial pressure in meristematic tissues of an intact eelgrass shoot during a light–dark transition experiment. The rapid (~45 min) establishment of a low steady state oxygen partial pressure in the dark strongly suggests that rates of oxygen transport between tissues and losses to respiration and external media are high (Redrawn from Greve et al., 2003).

oxygen partial pressure in leaves generated by photosynthesis create steep gradients from leaves to water column and less steep gradients from leaves to below-ground tissues. During darkness, the oxygen partial pressure in leaves declines below that of the water column, and the oxygen flux becomes directed from water to leaf, instead of vice versa (Greve et al., 2003). Although weaker than in the light, the gradient from leaf to rhizomes and roots persists during darkness ensuring a continuous supply to below-ground tissues.

Rapid changes in the oxygen content of meristematic tissues in the transition between leaves and rhizomes of eelgrass suggest that rates of internal oxygen transport and losses to the external media are high and that internal oxygen pools are relatively short-lived (Fig. 8; Greve et al., 2003). A thorough examination of oxygen losses in the submerged freshwater macrophyte *Egeria densa* (Sorrell and Dromgoole, 1987, 1988) showed that internal pools of oxygen were depleted rather slowly (up to 4 h) probably due to high resistance toward gas exchange between leaves and water column. Seagrasses may have more gas permeable leaves because time intervals between the occurrence of new steady state oxygen balances in both *Zostera marina* (Fig. 9; Greve et al., 2003) and *Cymodocea rotundata* (Pedersen et al., 1998) were less than 2 h after light–dark switches. One consequence of this apparently high permeability is that the internal pool of oxygen built up by photosynthesis during the day is insufficient to support night-time respiration of leaves, rhizomes and roots, in contrast to what is often supposed (e.g. Smith et al., 1984; Touchette and Burkholder, 2000).

Rapid internal transport of oxygen by passive diffusion from the leaves of *Zostera marina* to the meristematic region and further on to rhizome internodes is also demonstrated by changes in internal oxygen partial pressures after manipulation of water column oxygen concentrations during darkness (Fig. 9A). Water column oxygen was lowered stepwise from atmospheric equilibrium to zero, and after each step, new steady-state oxygen partial pressures were rapidly attained within the meristematic tissue and at two positions along the rhizome. An oxygen gradient persisted throughout the experiment with the highest oxygen partial pressure in the meristematic region and the lowest in the oldest rhizome internode. At a water column oxygen partial pressure corresponding to about 25% of air saturation the most distal rhizome internode became close to anoxic, but traces of oxygen were still observed in rhizome internode #3 and in the meristematic tissue reflecting a continuous transport of oxygen by passive diffusion.

The experiment with stepwise reduction in water column oxygen concentrations makes it possible to estimate the velocity of internal oxygen transport within the rhizome of *Zostera marina* (Fig. 9B). For each step, there was a consistent lag period between the time when water column oxygen had started to decline until changes in the oxygen partial pressures within the rhizome sections were recorded. The distance between the meristematic region and rhizome internode #4 was about 5 cm, and the traveling time for oxygen over that distance was 4–5 min clearly reflecting rapid gas phase diffusion.

C. Oxygen Transport by Mass Flow

Mass flow of lacunal gasses has been demonstrated for several emergent plants (Dacey, 1981; Armstrong and Armstrong, 1990; Brix et al., 1992), but major oxygen transport by mass flow likely requires through-flow provided by tissue contact with the atmosphere. In submerged plants, mass flow could theoretically occur on a small scale driven by internal pressurization generated from photosynthesis or by leaf movement due to waves or water current. However, gas phase diffusion should be sufficient to ensure oxygen transport in submerged plants as

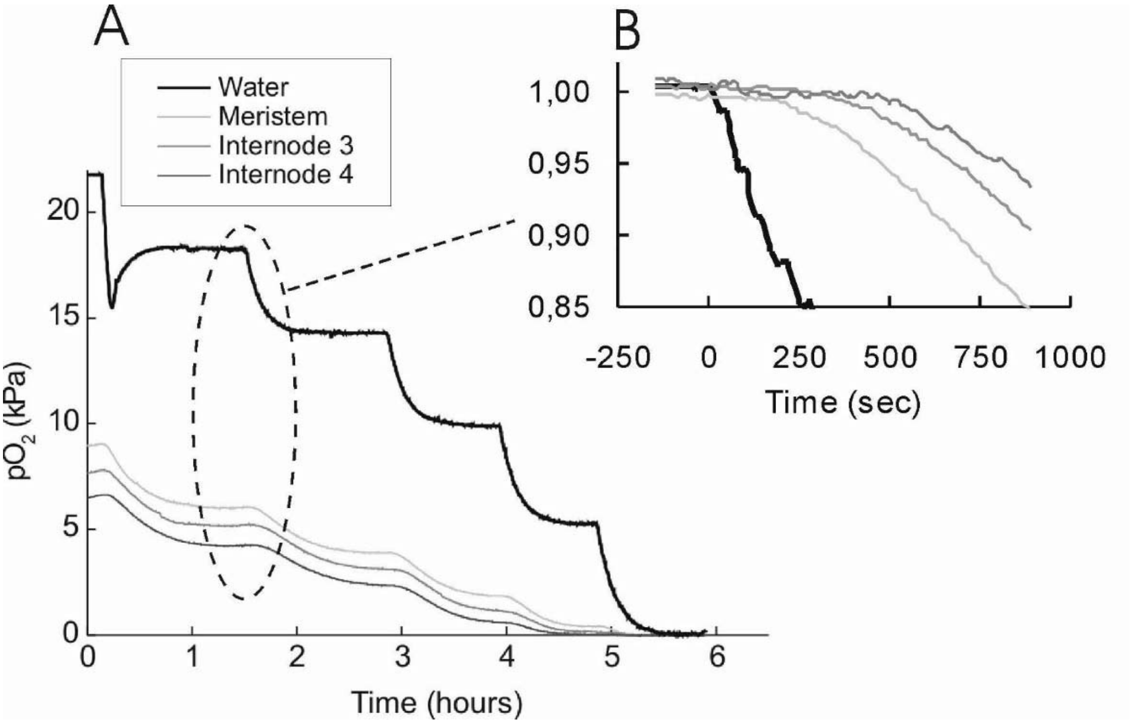

Fig. 9. (A) Internal oxygen partial pressure in eelgrass tissues as a function of water column oxygen content. The rapid establishment of steady states inside the tissues reflects the efficiency of internal oxygen transport by passive diffusion. (B) Relative changes in oxygen concentrations of the water column, the eelgrass meristem and of rhizome internodes #3 and #4 upon stepwise reduction of water column oxygen concentration. The lag period between changes in oxygen concentrations of the different tissues reflect traveling velocities within the lacunae of the rhizome. The distance between the meristematic tissue and internode #4 was about 5 cm (Pedersen, Borum and Binzer, unpublished).

convincingly argued by Sorrell and Dromgoole (1987, 1988).

Pressurization does take place in submerged plants (Sorrell and Dromgoole, 1987) and has also been observed in seagrasses (Roberts and Moriarty, 1987; Terrados et al., 1999). In the light, lacunal gas pressure above atmospheric pressure was built up in the horizontal rhizome of the Mediterranean seagrass, *Cymodocea nodosa* (Fig. 10). In a young rhizome internode lacunal gas pressure stabilized at around 15 kPa above atmospheric pressure. In an older internode of the same plant, steady state gas pressure in the light was consistently lower reflecting the existence of the internal pressure gradient, which is required to drive any mass flow. In the dark, lacunal gas pressure quickly fell to levels below atmospheric pressure and an inverse pressure gradient from the older to the young rhizome internode was established (Fig. 10). The pressure gradient could potentially generate a mass flow of oxygen from the young to the older internode in the light and thereby supplement diffusive oxygen transport to below-ground tissues, while in darkness, a possible mass flow would counteract diffusive oxygen transport to the roots. The existence of pressurization and pressure gradients does not reveal much about the importance of mass flow for internal oxygen transport. Relatively strong gradients may be formed with little mass flow, if the resistance to mass flow by the diaphragms/septa, regularly interrupting seagrass lacunae to prevent flooding (see section V A), is high. On the other hand, mass flow could play a role in gas transport under transient conditions with shifts from the dark to light and if leaf movements generate variable pressures within the leaves. These aspects deserve further investigation.

VI. *In Situ* Oxygen Variability in Seagrass

By use of microelectrodes, diel changes in the internal oxygen partial pressure of both *Zostera*

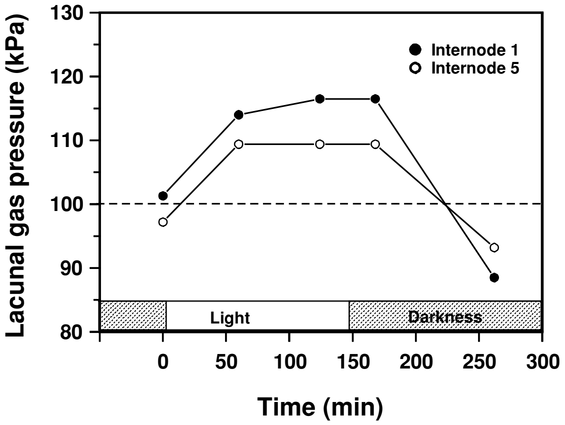

Fig. 10. Internal gas pressure in rhizome internodes of *Cymodocea nodosa* during a dark–light-dark transition experiment. In the light, gas pressures above atmospheric pressure were build up and a steady state pressure gradient occurred between the young rhizome internode #1 and the older internode #5. In the dark, an inverse gradient was formed at sub-atmospheric pressures (Redrawn from Terrados et al., 1999).

marina (Fig. 11; Greve et al., 2003) and *Thalassia testudinum* (Borum et al., 2005) have been assessed *in situ* under different environmental conditions. The oxygen content of eelgrass meristems followed similar temporal patterns and varied substantially over a diel cycle (Fig. 11). Internal oxygen partial pressures were above water column oxygen partial pressures and above atmospheric equilibrium in the afternoon at high surface irradiances and fluctuated systematically with changes in irradiance the following morning. In the dark, internal oxygen partial pressures declined steadily to low levels of about 15% of atmospheric equilibrium around sunrise. Similar patterns in plant oxygen contents have been recorded during other diel measurements on stands of *Zostera marina* (Borum, Pedersen and Binzer, unpublished) and of *Thalassia testudinum* (Borum et al., 2005).

As suggested from Fig. 11, oxygen partial pressures within the plants seem primarily dependent on changes in surface irradiance in the light and controlled by changes in water column oxygen concentrations at night. This suggestion is confirmed when internal oxygen partial pressures are plotted vs. surface irradiance in the light (Fig. 12A) and water column oxygen in the dark (Fig. 12B). In the light, the relationship resembles a typical photosynthesis–irradiance curve with increasing internal oxygen contents at low light reaching saturation at high light, while in the dark, plant oxygen contents are linearly related to the oxygen concentration in the water column. The oxygen content at high light is determined by the balance between the light-saturated oxygen evolution in leaves and the oxygen losses due to plant respiration and the oxygen efflux to the water

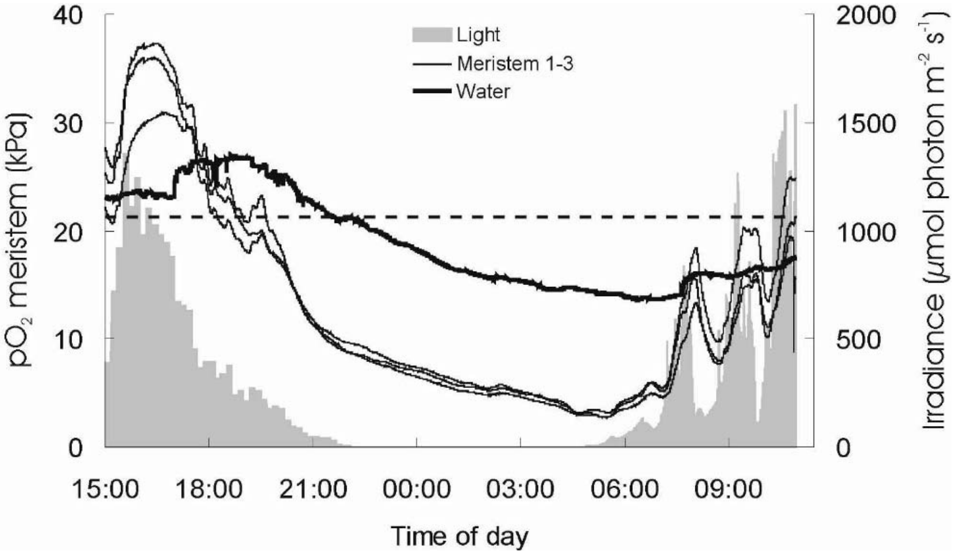

Fig. 11. Diel changes in surface irradiance and oxygen partial pressures of the water column and meristematic tissues of three eelgrass shoots measured *in situ*. During daylight, the fluctuating internal oxygen contents are intimately coupled to surface irradiance, while at night, changes in water column oxygen concentration seem to be the most important forcing factor controlling internal oxygen partial pressures (Borum, Pedersen and Binzer, unpublished).

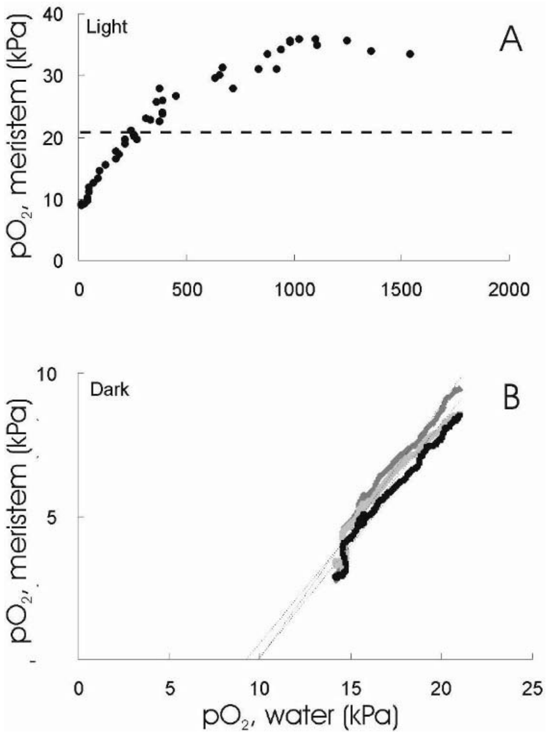

Fig. 12. Plant oxygen partial pressures from Fig. 11 plotted (A) vs. surface irradiance (data from afternoon), and (B) versus water column oxygen partial pressure for the dark period (Borum, Pedersen and Binzer, unpublished).

column and sediment. The baseline oxygen partial pressure at zero irradiance (Fig. 12A) and the linear relationship between plant and water column oxygen in the dark (Fig. 12B) are determined by the balance between oxygen supply from the water column and oxygen losses due to plant respiration and the oxygen efflux to the sediment.

In the tropical turtle grass in Florida Bay, diel changes in internal oxygen content, similar to those shown in Fig. 11, have been recorded at several sites. Here, internal plant content of oxygen varied not only with surface irradiance and water column oxygen but also with sediment composition and plant density (Borum et al., 2005). In a sparsely vegetated bed with a moderate content of organic matter in the sediment, the oxygen partial pressure in the meristematic tissues remained relatively high throughout the diel cycle, while in a dense stand with organically rich sediments, the meristematic tissues turned anoxic during darkness, and rhizome and root metabolism had to rely on anaerobic metabolism for several hours during the night. These observations suggest that the oxygen partial pressure inside these tropical seagrasses is significantly influenced by reduced oxygen supply from the water due to lower water flow velocity in dense seagrass stands and/or by higher oxygen losses due to higher respiratory oxygen demands of more organically rich sediments, at higher temperatures compared to temperate seagrasses.

VII. Anoxia and Seagrass Die-off

Insufficient oxygen supply to meristems and roots of seagrasses may have severe implications for seagrass growth and survival. Tissue anoxia impairs growth of roots, nutrient uptake and translocation of nutrients and carbohydrates (Smith et al., 1988; Zimmerman and Alberte, 1996), and the disappearance of the oxic microshield around roots and rhizomes normally provided by the radial oxygen loss allows the invasion of reduced phytotoxins from the sediment to the plant tissues. Periodical invasion of sulfide from the sediment into roots of wetland plants has been indicated by the composition of sulfur isotopes in the roots (Carlson and Forrest, 1982; see also Koch et al., Chapter 8), and invasion of gaseous sulfide into seagrass lacunae has been measured using microelectrodes both under laboratory and field conditions for *Zostera marina* and *Thalassia testudinum* (Pedersen et al., 2004; Borum et al., 2005). It is not known whether the events of sudden seagrass die-off, which have been reported for temperate and tropical seagrass beds (Robblee et al., 1991; Greve et al., 2003), are caused by poor energy availability during anaerobiosis, by accumulation of toxic plant metabolites or by invasion of toxic compounds from the sediment. All these phenomena, however, seem to originate from an insufficient supply of oxygen from leaves to the meristematic tissues or below-ground tissues. To reach a clearer understanding of the reasons for sudden seagrass die-offs, it is important to examine rates and mechanisms of oxygen transport in seagrasses further and to establish more direct links between oxygen dynamics and plant mortality (see also Koch et al., Chapter 8).

VIII. Summary

Measurements of oxygen variability and transport in seagrasses and other submerged plants are difficult to conduct and interpret due to the existence of several sources and sinks of oxygen driving internal transport at different rates depending on conditions in the water column and sediment. Oxygen release and transport in seagrasses have mostly been assessed by measuring oxygen changes in incubation chambers, but oxygen variability within the plants can be assessed at much higher spatial and temporal resolution using microelectrodes. Also planar optodes could be applied to describe oxygen release to the rhizosphere at higher spatial and temporal resolution.

Quantitatively, photosynthetic oxygen evolution is the most important source of oxygen for internal transport and aerobic metabolism, but passive diffusion of oxygen from the water column to leaves and below-ground tissues during darkness is also important, and this source is necessary for maintaining the oxygen supply to roots and rhizomes during dark periods of more than 1–2 h. The largest loss of oxygen from seagrasses is from leaves to water column during periods of high light and photosynthesis, but the continuous leakage of oxygen from roots and rhizomes to the anoxic sediment both during light and dark periods also represents a major sink to plant oxygen. During high photosynthesis and active plant growth, the respiratory oxygen consumption is much lower than oxygen release to the external media. However, the relative importance of respiration increases markedly with increasing temperature or at times of low photosynthetic rates. The internal transport of oxygen between leaves and below-ground tissues is most likely to be primarily driven by passive diffusion within the air-filled lacunae. Pressurization, however, does occur and may account for some internal oxygen transport especially during transient shifts between light and darkness. There is a need for more direct measurements of oxygen traveling velocities to elucidate the roles of passive diffusion vs. pressurization under different environmental conditions, and the possible coupling between internal oxygen dynamics and seagrass die-offs deserves further investigation.

Acknowledgments

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Chapter 11

Dynamics of Seagrass Stability and Change

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I. Introduction

To the casual observer, seagrass meadows often appear to be uniform landscapes with limited structure. Belying this appearance, seagrass meadows contain considerable structure and dynamics (cf. den Hartog, 1971). Seagrass meadows, at any one time, consist of a nested structure of clones, possibly fragmented into different ramets, each supporting a variable number of shoots. Thus, although apparently rather static, seagrass meadows are highly dynamic landscapes maintained through the continuous recruitment of new clones to the meadow, and the growth and the turnover of the shoots they contain. Therefore, the intense dynamics of seagrass ecosystems results from the combination of processes operating at various scales, which—if balanced—maintain a rather stable ecosystem. Often, however, the various processes responsible for meadow dynamics are either unbalanced or out of phase due to either natural causes or anthropogenic effects. Such imbalances result in changes in the meadows, which are sometimes readily evident, such as the case in catastrophic seagrass declines or are so subtle as to even elude quantification, such as may be the case in the gradual decline of slow-growing seagrass species (e.g. Marbà et al., 2003).

A proper understanding of these dynamics require, therefore, a basic understanding of contribution of the different relevant processes conforming the seagrass meadow. These processes are those affecting clonal growth, from the dynamics of apical meristems and the resultant shoots—the basic units of seagrass meadows—to that of the patches. Sexual reproduction is the primary mechanism of patch initiation, along with the dispersal of seagrass fragments, and the survival and growth of the patches is under strong environmental control. These processes and mechanisms will be discussed in this chapter to offer an overview of the processes responsible for the dynamics of seagrass meadows.

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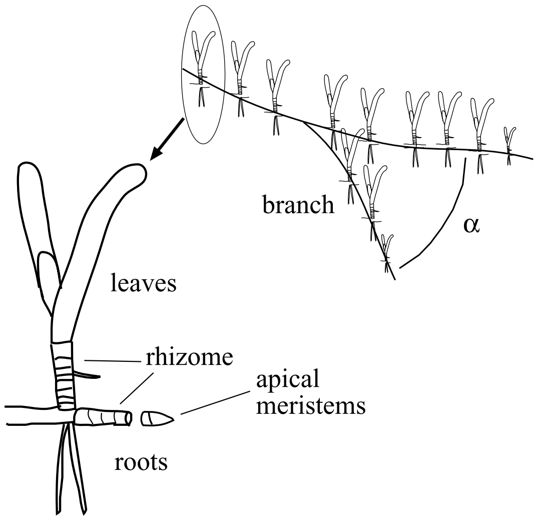


Fig. 1. Schematic representation of a shoot, the basic module of seagrass clones, containing leaves, grouped into leaf bundles, roots and a piece of rhizome, and a branching rhizome. α denotes the branching angle.

II. Components of Seagrass Meadows: from Apical Meristems to Meadows

Seagrasses are clonal plants, whereby the plant growth occurs through the reiteration of a basic set of modules, connected by rhizome material to develop the clone (Marbà and Duarte, 1998; Hemminga and Duarte, 2000). This basic module consists of a shoot, bearing a leaf bundle in all species except some *Halophila* species that have a leaf pair at each shoot (den Hartog, 1970), and a set of adventitious roots and a rhizome piece connecting them to neighboring shoots (Fig. 1). The reiteration of these modules is achieved through cell division at the apical rhizome meristem, which provides, therefore, the basis for seagrass clonal growth (Tomlinson, 1974). In addition, to produce new modules, the apical rhizome meristem may divide, producing a branch also containing an apical rhizome meristem, which extends the clone in a different direction (Fig. 1). Hence, an adequate representation of clonal growth patterns requires characterization of the size of the clonal modules and their organs, the spacing in between consecutive modules along the rhizome, the rhizome elongation rate and its branching rate, and angle (Fig. 1; Marbà and Duarte, 1998). There has been, therefore, considerable effort to quantify these properties across the seagrass flora (Tables 1 and 2).

Table 1. Mean and range of components of clonal growth of seagrass species. Based on data compiled by Marbà and Duarte (1998).

Trait	Mean	Min	Max
Rhizome elongation (cm year^{-1})	79	2	3.56
Horizontal rhizome branching rate (% of internodes)	5.8	0.06	25.97
Horizontal rhizome branching angle (degrees)	47	19	81

The components of clonal growth all range greatly across the seagrass flora (Table 1, range of variation of clonal properties across the seagrass flora), including significant plasticity within species (Pérez et al., 1994; Marbà and Duarte, 1998). However, much of this variability can be explained through allometric relationships between these components and module size, as represented by either shoot weight or rhizome diameter (Duarte, 1991; Marbà and Duarte, 1998; Hemminga and Duarte, 2000). Hence, small seagrasses show faster clonal growth rates than large species (Table 2), which tend to

Table 2. Average rhizome elongation rates of seagrass species. Based on data compiled by Marbà and Duarte (1998).

Species	Rhizome elongation (cm year^{-1})
Amphibolis antarctica	20
Amphibolis griffithii	4
Cymodocea nodosa	40
Cymodocea rotundata	210
Cymodocea serrulata	153
Enhalus acoroides	3
Halophila decipiens	215
Halophila hawaiiana	89
Halophila ovalis	356
Heterozostera tasmanica	103
Halodule uninervis	101
Haludule wrightii	223
Posidonia angustifolia	12
Posidonia australis	9
Posidonia oceanica	2
Posidonia sinuosa	4
Phyllospadix scouleri	17
Phyllospadix torreyi	26
Syringodium filiforme	123
Syringodium isoetifolium	109
Thalassia hemprichii	54
Thalassia testudinum	69
Thalassodendron ciliatum	16
Thalassodendron pachyrhizum	3
Zostera marina	26
Zostera noltii	68

grow slowly (Duarte, 1991; Marbà and Duarte, 1998; Hemminga and Duarte, 2000). On the basis of the existence of such allometric relationships, the seagrass flora has been described as composed of scale models of a generic design (Marbà and Duarte, 1998). Whereas this statement holds if examining individual properties, the simultaneous variation in average clonal properties across species renders clonal patterns complex, thereby resulting in contrasting growth strategies across species.

The simplest models of clonal growth could not elucidate these differences for they portrayed clonal growth as a simple radial growth process, with circular-shaped clones extending at a constant radial growth rate equivalent to the average rhizome elongation rate of the modeled species (Duarte, 1995; Kendrick et al., 1999). However, comparison of the resulting prediction of colonization rates with observed dynamics provided evidence that clonal growth does not proceed at a constant rate, but that it accelerates over time (Kendrick et al., 1999). More elaborate models of clonal growth used all components of clonal growth, as represented by their average value and observed within-species variability, to examine the development of clonal networks (Marbà and Duarte, 1998; Sintes et al., 2005. Models using clonal growth rules to simulate clonal growth provided evidence that, as suggested by field observations (Vidondo et al., 1997; Kendrick et al., 1999), this is a strongly non-linear process (Marbà and Duarte, 1998; Sintes et al., 2005). The radial growth of seagrass clones accelerates from very low values at the early stages of growth to high rates (Marbà and Duarte, 1998; Sintes et al., 2005), equaling the extension rates of runners (i.e. rhizomes extending outside seagrass patches), by the time they reach highly compact structures (Fig. 2). The efficiency of space occupation, as described by the increase in patch size achieved for a given rhizome production, declines sharply with increasing clonal size (Sintes et al., 2005). The applicability of these models, developed using *Cymodocea nodosa* as the model species, to other species is yet to be assessed.

Whereas fast-growing seagrasses have been assumed to display a guerrilla strategy compared to the more compact, ‘phalanx’ growth strategy assumed for larger, slow-growing species, analysis of model results indicate that these expectations do not hold (Marbà and Duarte, 1998). The broad branching angles of the fast-growing, small seagrass species (e.g. *Zostera noltii*) lead to a compact growth, following a spiral pattern around the origin of the clone, whereas the narrow branching angles of large-slow-growing seagrasses project them at relatively larger distances for a given investment in rhizome material, generating a guerrilla-like pattern but over a long period of time (Fig. 3).

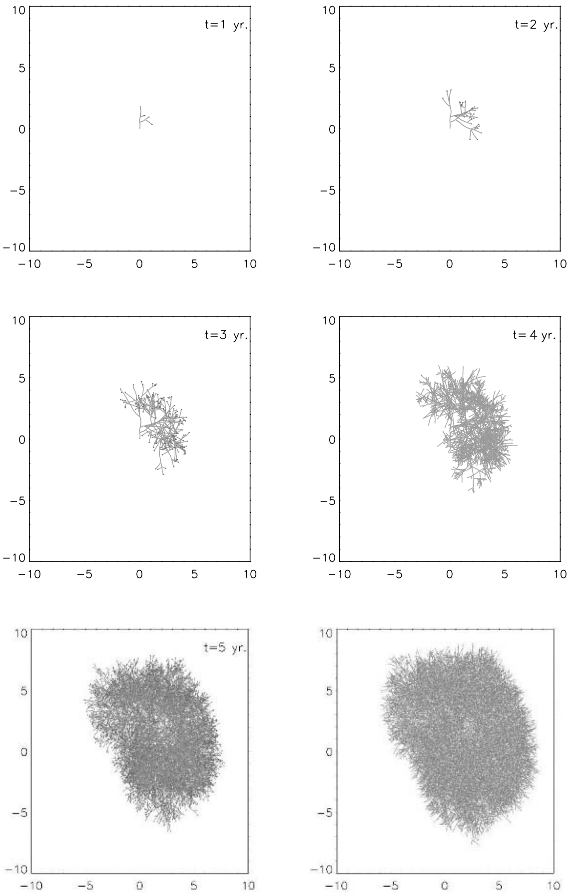
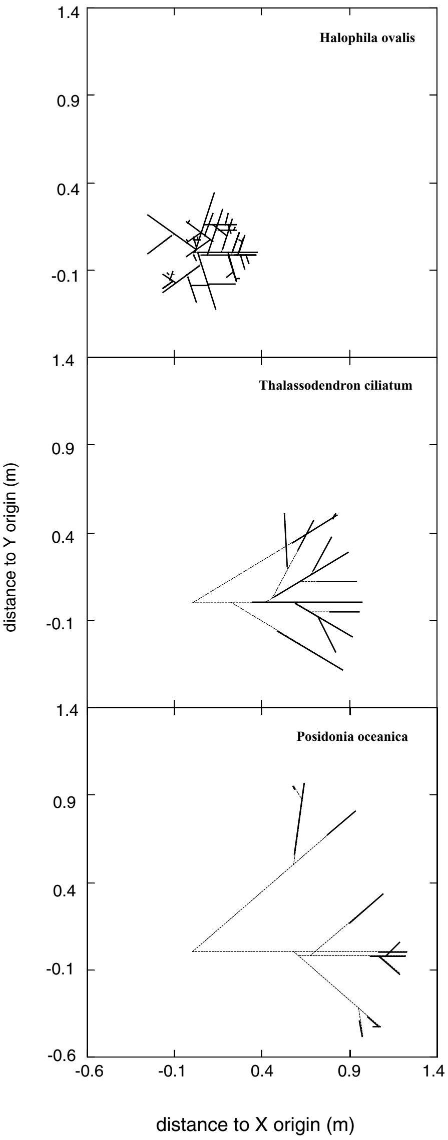


Fig. 2. The shape of modelled *Cymodocea nodosa* clones of different ages. From Sintes et al. (2005)—with permission.

Present depictions of clonal growth patterns cannot, however, be used to infer the resulting structure of the meadows, for these models examine the growth of individual clones and do not consider possible interferences from neighboring clones. Moreover, there is evidence that there is a limit to the maximum density of seagrass stands (e.g. Duarte and Kalff, 1987; Marbà and Duarte, 2003), so that the presence of neighboring clones is expected to reduce the growth of adjacent clones. Indeed, models of seagrass clonal development can only reproduce the internal density of seagrass clones if an exclusion



time = 0.10 yr

	produced	alive
rhizome (m)	5.7	5.4
number of shoots	336	262

time = 6 yr

	produced	alive
rhizome (m)	5.5	3.5
number of shoots	201	59

time = 55 yr

	produced	alive
rhizome (m)	5.3	1.7
number of shoots	191	38

Fig. 3. The simulated spread of clones of different seagrass species predicted on the basis of their basic growth rules: horizontal rhizome elongation rate, and branching rules (probability and angle). The graphs depict the clonal topography after producing ca. 5 m of rhizome for three contrasting seagrass species (*Halophila ovalis, Thalassodendron ciliatum*, and *Posidonia oceanica*). The time required to develop the networks, and the rhizome length, and number of shoots produced and surviving since initiation of clonal spread are indicated. Dashed lines show the spatial distribution of the rhizomes and shoots produced, and continuous ones the distribution of surviving rhizomes and shoots. Reproduced from Marbà and Duarte (1998)—with permission.

area, or per capita space, which is unlikely to be occupied by another shoot, is defined around each shoot (Sintes et al., 2005), thereby supporting empirical evidence for architectural-determined seagrass density (Marbà and Duarte, 2003). The role of density-dependence in regulating clonal growth and space occupation in seagrasses is, however, insufficiently developed at present. Hence, whereas the expected dynamics of colonizing clones are adequately represented by existing knowledge and rate estimates, the dynamics of clones within established meadows is not sufficiently understood as yet to allow reliable models of meadow development and dynamics to be formulated. Moreover, the role of environmental factors, prominently hydrodynamics in shaping the landscape produced (cf. Bell et al., Chapter 26), is

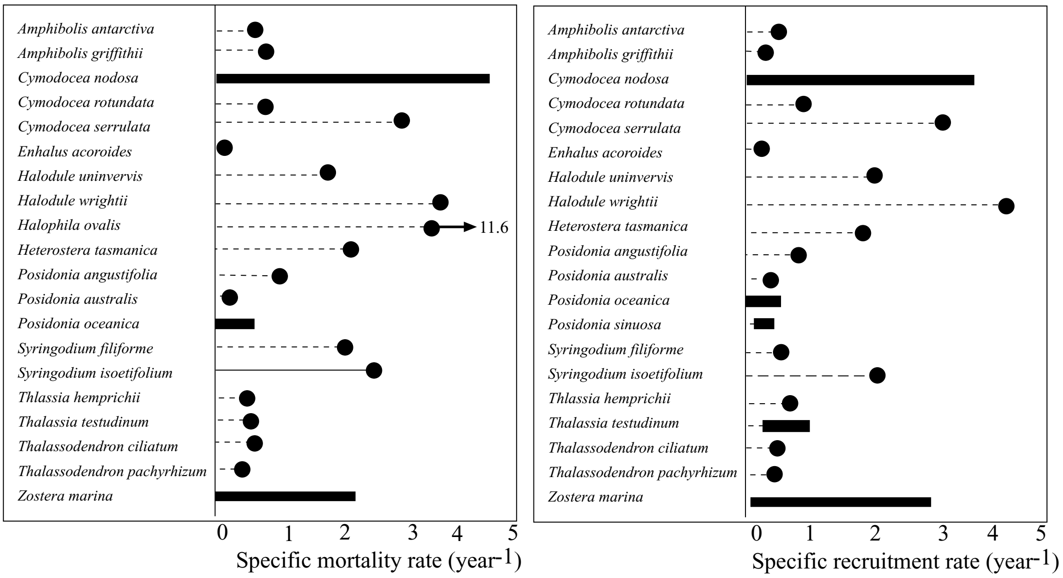


Fig. 4. Reported shoot mortality and recruitment rates for seagrass species. Solid circles represent average values, and bars extend across reported ranges. Data from tables in Hemminga and Duarte (2000).

also not captured as yet by models of how clonal growth develops into meadows.

III. Shoot Dynamics

A. Shoot Recruitment: Vegetative and Sexual

Shoot recruitment is the addition of new individuals to the population occurring by the vegetative production of new shoots through clonal growth or by the recruitment of new genets through production and germination of seeds or fragments. Uprooted shoot modules may also act as recruitment units (Ewanchuk and Williams, 1996; Reusch, 2001; Campbell, 2003) although the successful establishment and survival of such vegetative fragments inside established vegetation has yet to be documented. Vegetative shoot recruitment proceeds at highly variable rates and is largely a species characteristic although individual species also show plastic response of clonal growth to ambient conditions. Hence, vegetative shoot recruitment does not proceed at constant rates in time and space and experimental studies have demonstrated reduced rates of shoot recruitment in nutrient and light limited stands (Gordon et al., 1994; Pérez et al., 1994; Agawin et al., 1996; Ruíz and Romero, 2001). In dense stands light also tends to impose an upper limit to shoot recruitment such that rates may be constrained by the density of neighbouring shoots, thereby avoiding overcrowding of the populations (Duarte and Kalff, 1987; Olesen and Sand-Jensen, 1994a). Variability in clonal growth also has a seasonal pattern, particularly in temperate regions, with shoot formation rates proceeding slowly during winter when growth is restricted by adverse growth conditions and rapidly in early summer concomitant with increasing temperature and light (Bigley and Harrison, 1986; Marbà et al., 1996a). Accordingly, shoot formation rates are influenced by resource availability imposing a limit to overall rates of seagrass growth but the substantial plasticity observed may also be an important component of their capacity to acclimate to growth under a range of environmental conditions.

The high variability across species in rates of vegetative shoot formation scales to size such that the time interval between the production of consecutive shoots on the horizontal rhizome is much longer (months) in large seagrass species than in small species (days) (Duarte, 1991; Marbà and Duarte, 1998; Marbà and Walker, 1999; Hemminga and Duarte, 2000). Hence, the average specific vegetative recruitment rates of new shoots into seagrass populations proceed at rates spanning more than 10-fold from the large seagrass species *Enhalus acoroides* (0.26 year^{-1}) to the small species *Halodule wrightii* (4.81 year^{-1}; Fig. 4). The variability within a species can be as large as that across the seagrass flora, and there can be considerable variability between years and sites in the rate of recruitment of new shoots into populations (Durako, 1994; Marbà et al., 1996b). Hence, for the relatively large species *Thalassia testudinum*, characterized by moderate rates of vegetative shoot formation, annual recruitment can vary from 0.01–1.30 year^{-1} among populations (Peterson and Fourqurean, 2001). Despite the very low rates of vegetative shoot production in the large seagrass species, however, the much longer shoot life-span of these species ensure a close balance between shoot recruitment and losses in stable populations.

Vegetative rather than sexual recruitment is generally considered the primary mechanism to the maintenance of shoot density within closed seagrass vegetation. Firstly, the sexual reproductive effort is low in many seagrass species, the proportion of shoots that flower being generally less than 10%, and seed set occur irregularly in many populations (Duarte et al., 1997b; Durako and Moffler, 1985; Marbà and Walker, 1999; Campey et al., 2002). Secondly, large plants suppress the growth of small ones, such that the entry of new sexual recruits inside areas occupied by adult genets can be expected to occur only when established individuals are lost and vacate space. Most information of seedling recruitment and establishment come from studies performed outside established vegetation where it is less problematic to discern sexual recruits from shoots derived from already established clones. However, these studies suggest low survival rates of seeds and newly established seedlings (Hootsmans et al., 1987; Duarte and Sand-Jensen, 1990a; Harrison, 1993; Kirkman, 1998; Kaldy and Dunton, 1999; Balestri and Cinelli, 2003) supporting the contention that successful sexual recruitment events must be rare within closed vegetation.

Even though vegetative shoot formation is the dominant reproductive mode in seagrass meadows, large differences in recruitment strategies among species (Inglis, 2000) and considerable variation in spatial and temporal extent of seed production suggest that sexual recruitment can play a potential role in meadow maintenance, particularly in populations where the risk of adult mortality is high, leaving open space available for seedling establishment and growth (see Orth et al., Chapter 5). In the extensively studied seagrass *Zostera marina*, the reproductive effort is highly plastic and populations adopting an annual growth strategy, typically in physically harsh environments, produce significant number of seeds (>20,000 seeds m^{-2}) and regenerate completely from seeds each year (Harlin et al., 1982; Phillips et al., 1983; Phillips and Backman, 1983; van Lent and Verschuure, 1994). Also, the ability to accumulate stocks of persistent seeds inside the parent meadow of some of the small, shorter-lived seagrass species producing poorly-dispersed seeds (e.g. *Cymodocea nodosa*; Terrados, 1993 and *Halophila* spp; McMillan, 1988; Kuo et al., 1993; Preen et al., 1995; Kenworthy, 2000; also see Ackerman, Chapter 4 and Orth et al., Chapter 5) may promote meadow persistence following natural senescence of plants or disturbances by recruiting new sexual propagules. Hence, the relative importance of sexual and asexual shoot recruitment to meadow maintenance may vary considerable among species and environments. While sexual recruitment can be critical for meadow maintenance in highly disturbed and extreme environments inhabited by small shorter-lived seagrass species, the quantitative importance of sexual recruitment in meadows of larger and longer-lived species is low relative to asexual recruitment and seeds primarily contribute to the establishment of new patches.

B. Shoot Mortality

Specific shoot mortality rates range greatly both across seagrass species (Hemminga and Duarte, 2000) and across meadows for any one species (Marbà et al., 1996b; Peterson and Fourqurean, 2001), from lowest values of 0.06 year^{-1}(i.e. 6% of shoots dying in a year) for a stand of the long-lived Mediterranean seagrass *Posidonia oceanica* to a maximum estimated mortality rate of 4.47 year^{-1} for *Cymodocea nodosa* (Fig. 4). These shoot mortality rates incorporate two additive components, a baseline mortality corresponding to an internally-controlled mortality rate necessary to maintain shoot turnover, and a component derived from stresses and disturbances to the meadows.

Shoot mortality is not only a prominent component of the dynamics of seagrass meadows, but is indeed a necessary one. In an established, steady meadow, the continuous recruitment of seagrass shoots resulting from branching processes cannot be sustained without a parallel mortality of shoots, as crowding would otherwise impare recruitment. Shoot mortality is, however, insufficiently understood, and the causes of shoot mortality have not been elucidated as yet. Shoot mortality is a necessary component of the maintenance of stable seagrass meadows, so that the presence of a stress factor need not be invoked to account for shoot mortality. These thoughts suggest that, to some extent, shoot mortality should be considered a component of clonal integration, such that a clone may selectively 'decide' to cease the activity of a particular leaf-producing meristem, thereby causing shoot death. Whereas the activation of seagrass meristems in response to disturbance, such as increased branching rates (i.e. shoot production) in response to clipping of apical rhizome meristems (Terrados et al., 1997), have been examined, the internal controls on loss of meristematic activity have not been addressed, as yet. More importantly, there is a need to examine what factors may cause the death of apical meristems, which would reduce shoot recruitment. The understanding and capacity to predict meristematic activity may provide the capacity to detect stress and forecast mortality before this is reflected in shoot density changes.

Hence, most knowledge on the controls on shoot mortality derives from examination of stress and disturbance factors. Reduced water and sediment quality leads to shoot mortality, often resulting in catastrophic seagrass loss through multiple factors. Deterioration of water quality leads to seagrass mortality through light limitation and unbalanced plant carbon budgets (e.g. Gordon et al., 1994; Ruiz and Romero, 2001). Shoot mortality as a consequence of reduced light penetration has been reported at the depth limit of seagrass meadows (Krause-Jensen et al., 2000), and confirmed by shading experiments (Gordon et al., 1994; Ruíz and Romero, 2001). Increased nutrient inputs have also been shown to be associated to high mortality rates (Pérez et al., 1994). Deterioration of sediment conditions, such as increased sediment anoxia and sulfide production has been shown to lead to seagrass mortality, although the responses vary greatly across species (Terrados et al., 1999). Water column hypoxia, also derived from excessive organic inputs, has also been identified as a factor affecting the health of leaf-bearing meristems, eventually causing shoot death (Greve et al., 2003). Sediment disturbance, such as excessive burial and sediment erosion, also causes shoot death by killing meristems, altering clonal integration, and, when extreme, creating topographical barriers (Marbà and Duarte, 1994, 1995; Duarte et al., 1997a). Physical disturbance is also an important source of shoot mortality, through uprooting of the plants during storms or due to human activities such as anchoring, dredging, anchor damage, and trawling (Duarte, 2002). Biological disturbance may also generate substantial seagrass mortality (e.g. Orth, 1975).

C. Shoot Demography

It is possible to estimate the age of individual shoots of most seagrass species because there is a relatively constant rate of production of new leaves on a shoot, called the **plastochron interval**. Each leaf leaves a distinctive scar on the short shoot at the node, so it is possible to count the number of leaves produced over the lifespan of an excavated shoot and multiply this number of leaves by the plastochron interval to estimate the age of the shoot (Patriquin, 1973; Duarte et al., 1994). Once recruited into the population, shoots of different species have different average lifespans. Shoots of the small, fast-spreading species, like *Halophila* spp., have an average lifespan of only a month or so, and a maximum age of a few months (Table 1). In contrast, the shoots of the larger, slower-spreading species like *Posidonia* spp. and *Thalassia* spp. have average life expectancies of a few years, with some shoots surviving for decades. A genetically individual plant may be much older than individual short shoots, since most seagrasses exhibit monopodial or sympodial growth. As a rhizome grows through the soil and produces new shoots, each successive shoot is necessarily younger than the previous shoots. Older shoots may eventually senesce, but their progeny shoots may continue to thrive and extend away from the point where a seedling originally produced the genetically individual plant. Theoretically, genetic individuals could be as old as the origin of the species, even though individual shoots can only survive a few decades at most.

Seagrasses, as angiosperms, are all capable of sexual reproduction through flowering and seed production (although sexual structures have not been observed for all species, e.g. Jewett-Smith et al., 1997). As long as seeds result from the fertilization of an ovule by pollen from another genetically distinct individual, the plant originating from that seed is genetically distinct from others in the population. Once a seedling becomes established in a seagrass meadow, it begins to grow up by the production of photosynthetic leaves, but also out by the production of new plant modules consisting of a length of rhizome, associated roots, and a shoot. The branching pattern created by the production of new modules varies from many-branched plants that expand almost equally in two dimensions (e.g. *Posidonia oceanica*) to plants that extend almost exclusively linearly through space (e.g. *Thalassia testudinum*). Eventually, through the action of either senescence of modules or disturbance, these individuals can become physically separated so that what was once one plant can become many isolated plants—but all of these plants are genetically identical—i.e. they are parts of the same genetic individual (i.e. genet).

So, when studying the dynamics of seagrass populations, it is important to keep in mind that what appears above the sediments as a shoot is likely connected to many more shoots underground. And, merely because two shoots do not share a common connection somewhere under the sediments is no indication that these shoots are genetically different. In fact, there is molecular evidence for genetically identical shoots of *T. testudinum* separated by over 3 km in an otherwise genetically diverse, continuous seagrass bed (Davis et al., 1999). A more thorough discussion on this topic is provided in Waycott et al. (Chapter 2).

New genets can enter a population not just through successful seedlings, but also as adult plant fragments that may drift into a population from some distant source (Setchell, 1929). Seagrasses can float and survive for extended periods out of the sediment; apparently viable modules of the tropical seagrass *Thalassia testudinum* can occasionally be found on the temperate beaches of the North Carolina in the US (JWF, pers. observ), over 1000 km from the nearest known *T. testudinum* populations. Seagrass shoots can survive for months in the water column, but the ability of detached shoots to survive when transplanted decreases with time in the water column, limiting the potential of drifting adult plants to establish new seagrass beds (Ewanchuk and Williams, 1996). Floating seagrass shoots not only have some potential to become reestablished and expand via asexual reproduction, but they can also carry viable seeds (Harwell and Orth, 2002; Orth et al., Chapter 5) and epiphytes (Worcester, 1994) to distant locations. The role of vegetative fragments as vectors for colonization has likely been underestimated in seagrass ecology, as these are rare events, that challenge direct observation, although direct evidence of widespread establishment by fragments has been recently reported (Campbell, 2003).

Although there are mechanisms to provide genetically unique recruits to seagrass populations, the importance of these mechanisms in producing new shoots in seagrass beds is considered low compared to the asexual ramification of plant modules by clones already extant in populations (Tomlinson, 1974). For most species, observations of successful seedling recruitment are rare (Orth et al., Chapter 5). However, the study of sexual recruitment in established populations is complicated by the difficulty in distinguishing whether shoots are derived from a single seed or from fragmentation of a larger clone (cf. Waycott et al., Chapter 2). Moreover, it is possible that the perception that successful seedling recruitment is a rare event may be dependent on insufficient observational effort, as this process may occur over significant spatial and temporal scales that challenge conventional sampling strategies.

D. Predicting Population Dynamics Using Shoot Demography

Most monitoring programs are inefficient at detecting and predicting change in shoot density, because such change can occur either precipitously (e.g. Robblee et al., 1991) or be too gradual to be detected within the typically broad error margins of density and cover estimates used in most monitoring programs (Heidelbaugh and Nelson, 1996). There is, therefore, a demand for approaches to quantify the components of seagrass population dynamics with the aim of allowing an evaluation of their status and an ecological forecast of possible future trends. Recently, the analysis of age structure data to infer population growth rate has been applied to seagrass beds using what has come to be known as the 'reconstructive technique' (Duarte et al., 1994), which has been applied to multiple species since (e.g. Kenworthy and Schwarzschild, 1998; Marbà and Walker, 1999; Guidetti, 2001; Peterson and Fourqurean, 2001).

Population dynamics reflect the balance between immigration, emigration, recruitment, and mortality, and the various factors that affect these gains and losses. For any closed population, the population growth rate per individual (r) is the difference between the per capita birth rate (Recruitment, R) and death rate (Mortality, M):

$$r = R - M \tag{1}$$

Knowing R and M, then, would allow for predictions of r. In concept, it should be a simple procedure directly to observe the production of new shoots and the death of others from a regularly-visited portion of a seagrass meadow. In practice, however, these observations have proven difficult to make because of the multiple visits required, the substantial time required to mark shoots in very dense, often deep stands, and the extended life span of many of the target seagrass species (e.g. *Posidonia* spp, *Thalassia* spp; cf. Hemminga and Duarte, 2000).

Within the limits imposed by some simplifying assumptions, it is possible to estimate R and M by analyzing the age structure of a population of seagrass shoots. The model generally used by seagrass ecologists (cf. Duarte et al., 1994; Peterson and Fourqurean, 2001) to estimate M from age structure data is:

$$N_x = N_0 e^{-Mx} \tag{2}$$

where N_x is the number of shoots in age class x and N_0 is the number of shoots recruited into the population (cf. Duarte et al., 1994). But, the rather restrictive assumptions of applying this model to seagrass shoot age structure data (Jensen et al., 1996; Kaldy et al., 1999; Ebert et al., 2002) require caution and an understanding of the implications of violations of these assumptions in application. Most importantly, this analysis assumes a stable age distribution (and, therefore, that $R = M$), a condition which cannot be verified a priori, and age-independence of R and M. This approach has been successfully applied (constrained by the same assumptions) to a wide variety of organisms, for example: mosses (Økland, 1995); marsh plants (Sutherland and Walton, 1990); bamboo (Taylor and Zisheng, 1993); mangroves (Duarte et al., 1998); terrestrial trees (Szeicz and MacDonald, 1995; Kelly and Larson, 1997). In fisheries research, analyses such as these are called ‘catch curve’ analyses (Ricker, 1975; Quinn and Deriso, 1999) and have been widely applied [e.g. larval sciaenids (Flores-Coto et al., 1998); tropical gobies (Kritzer, 2002)].

In the case where $r \neq 0$, and therefore $R \neq M$, application of Eq. (2) is not appropriate (Ebert et al., 2002). Instead, a more general model of the form:

$$N_x = N_0 e^{-(M+r)x} \tag{3}$$

is appropriate (Fourqurean et al., 2003). But, since the methods explicitly assume that M and R have remained constant over the lifespan of the oldest individuals in the population, how can this method logically be used to predict changes in r for the population? In reality, using a regression approach to estimate N_0 and R assumes that M and R have had no trend over the lifespan of the oldest shoots in the population, with year to year random variation around some mean value of M and R. So not only does the regression approach result in an estimate of the long-term mean R, but it provides statistical confidence limits for this estimate (Fig. 5). Hence, whereas the reliability of the estimates of R and M are dependent on the validation of the assumptions, which are always cumbersome, relevant information can still be extracted which is informative of the demographic dynamics of the populations. Similarly, forecasts derived from the examination of past demographic dynamics have to be taken with caution, provided that there is no guarantee that the underlying rates will remain constant in the future. This is however, a limitation inherent to any forecasting approach.

Besides this estimate of a long-term average recruitment rate, the age structure also yields an estimate of the recruitment for the year the population was sampled (R_0):

$$R_0 = \ln N_t - \ln N_{x>0} \tag{4}$$

where N_t is the total number of shoots in the population and $N_{x>0}$ is the number of shoots older than 1 year (Duarte et al., 1994; Short and Duarte, 2001).

From each age distribution, then, come two estimates of $R : R_0$, which is an estimate of the current recruitment rate, and the long term mean R. If one assumes no trend in M over the lifespan of the oldest shoots in the population, then a comparison of these two estimates can predict whether r (Eq. 1) for the current year is different from the average r over the lifespan of the oldest individuals in the population. Because the regression analysis provides confidence limits about the long-term mean R, such differences

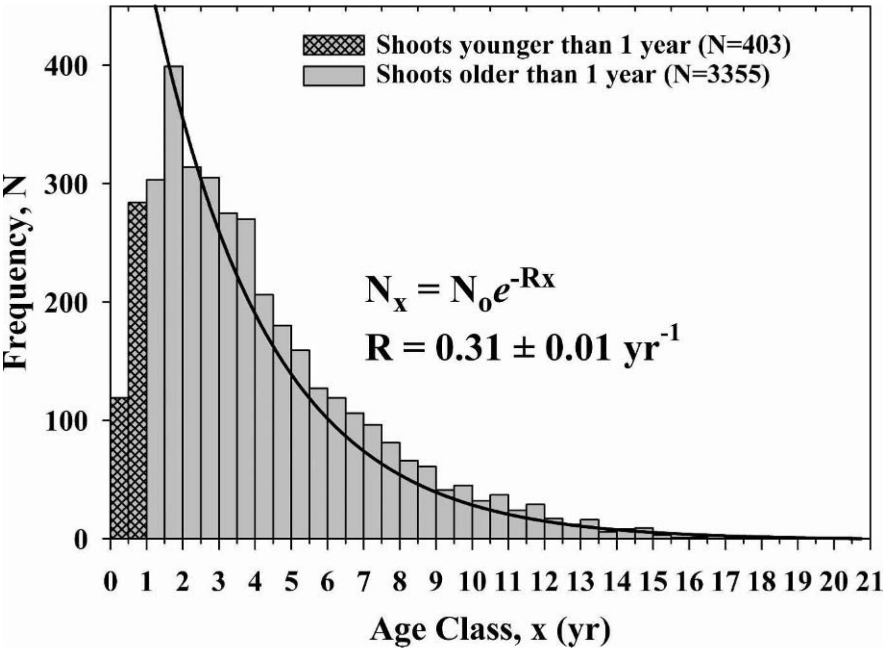


Fig. 5. Graphical depiction of the techniques used to calculate demographic information from age structure data. These data are ages of 3,758 short shoots (N_t) of *Thalassia testudinum* collected from south Florida in 2001. The current year's recruitment, R_0, = ln(3,758) − ln(3,355), or 0.11 year^{-1}. The exponential decay model indicates the long-term average R to be 0.31 ± 0.01 year^{-1}, indicating that recruitment in the year the shoots were collected (R_0) is significantly less than the long-term average recruitment. If the size of the population has been stable over the lifespan of the oldest shoots in the population (20 year in this case), then the long-term average R = long-term average M, and therefore we should expect this population to shrink by 20% this year (i.e. $r = R_0 - M$, or 0.20 year^{-1} = 0.11 − 0.31 year^{-1}).

can be tested statistically—but it should be noted that the accuracy of the prediction of the long-term mean R is dependent on the number of age classes, so that the method will derive more robust estimates for long-lived species (Fourqurean et al., 2003).

In addition to the comparison of present recruitment (R_0) relative to the long-term mean recruitment, ecologists can, through a residual analysis of the age class distribution against the assumed exponential decline in shoot number with increasing age (cf. Durako and Duarte, 1997), detect particularly bad and good years for the population in the form of fewer or greater shoots than expected for a particular age class. These inferences are more robust as the sample size used to build the age distributions increases, and reasonable estimates can be obtained at sample sizes in excess of 200–300 shoots. Examination of seagrass shoot age distributions provide useful assessments of the status of the stands and ecological forecasts, which inform of the likely trends in the population—but not numerical predictions, which predict the actual population size—of the future trends of the stands, assuming that the relation between the present year's R_0 and the long-term mean R were to persist. Improved forecasts or predictions require direct estimates of dynamic population parameters.

By following the 'birth' and death of shoots in tagged populations, direct estimates of M, R, and r can be derived (Short and Duarte, 2001), free of the assumptions required to derive estimates from age distributions. Direct censuses, however, are demanding of time and effort, for shoots have to be tagged individually in the field and relocated repeatedly. Moreover, individual tagging is difficult for small, fragile species, such as *Zostera noltii*, as well as in adverse environments, such as very deep or very turbid ones, and is easiest for longer-lived species, such as *Posidonia oceanica* and *Thalassia testudinum*,. Large-scale assessment of seagrass population dynamics through direct censuses is, however, possible, as demonstrated by Marbà et al. (2003).

IV. Clones and Patch Dynamics

A. Processes of Patch Formation

The spatial structure of seagrass populations is highly variable among sites ranging from extant, nearly continuous meadows to meadows that are highly fragmented and arranged into a mosaic of discrete patches. Patchy seagrass vegetation often reflects processes of recovery from disturbances, whether natural or human-induced, that occurred at different times in the past, as well as the particular hydrodynamic conditions of the seagrass habitats (cf. Bell et al., Chapter 26). Seagrass meadows have, therefore, not only spatial but also temporal dynamics involving the continuous recruitment, expansion, and mortality of patches. Hence, knowledge of these dynamic properties is essential to gain insight into the dynamics and persistence of seagrass populations.

Patches may result from fragmentation or colonization processes. Loss of seagrass cover may lead to fragmented beds resulting in a patchy, rather than continuous meadow distribution. Alternatively, patches may result from a colonization process, where propagules, whether established seeds or vegetative fragments initiate clonal growth, thereby producing a patch. Patch formation through seedling establishment has been well documented (e.g. Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997), although estimates of patch formation rates are still few. In contrast, patch formation through the anchoring of detached vegetative fragments has received limited attention (e.g. Campbell, 2003), although it may be an important process for seagrass patch formation.

Seedling establishment is a precondition but not a sufficient condition for patch formation, as available evidence suggests that many seedlings may die without ever producing patches (e.g. Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994; Olesen et al., 2004). For instance, a study of a *Cymodocea nodosa* population growing in a patchy lagoon showed that only small fractions of established seedlings initiated patch formation through clonal growth (Duarte and Sand-Jensen, 1990a). Failure to initiate clonal growth was attributed, in this particular population, to nutrient limitation (Duarte and Sand-Jensen, 1996).

B. Patch Growth and Loss

Seagrass patch growth proceeds by the horizontal extension of rhizomes at the patch edge and the subsequent branching and vegetative production of new shoots at the rhizome apex to fill out the open space between expanding rhizomes. The branching frequency and the angle between the horizontal rhizome and the rhizome branches that are formed on it are, therefore, important determinants of the capacity to spread in two dimensions (Marbà and Duarte, 1998). However, the main controlling factor on the patch growth rate is the elongation of horizontal rhizomes, extending the patch through its periphery. Realized patch growth rates may be lower than the potential rates set by rhizome extension rate whenever sediment dynamics and hydrodynamics interfere with plant growth or create disturbance (cf. Bell et al., Chapter 26).

The elongation rate of horizontal rhizomes is species specific (Table 2) and range from about 2 cm year^{-1} in the large slow-growing species as *Enhalus acoroides* and *Posidonia oceanica* to more than 300 cm year^{-1} in small fast-growing species as *Halophila ovalis* (Duarte, 1991; Marbà and Duarte, 1998). The close, negative scaling between rhizome elongation rates and seagrass module size, suggests that shoot size is a strong predictor of patch extension through clonal growth for the different seagrass species.

The maximal rate of rhizome growth sets the upper rate of patch extension possible although this capacity is not necessarily realized in natural patches. Seagrasses display considerable plasticity in formation rates and size of modules (Duarte, 1991). Variability in rhizome growth often has a distinct seasonal pattern, particularly in temperate and subtropical climates, where rhizome growth is minimized during winter as a result of low light and temperature conditions. Rhizome growth can also be expected to respond to resource availability, e.g. through enhanced elongation rates in deep growing stands, thereby reducing internal self-shading by increased distance between neighboring shoots (Olesen et al., 2002). This response pattern does not apply to all species, however, and experimental evidence is needed to evaluate the adaptive significance of seagrass rhizome growth to various environmental conditions.

Patch growth may also be affected by intrinsic factors and has been found to accelerate with patch size and age (Duarte and Sand-Jensen, 1990a; Vidondo et al., 1997). In a study of *Cymodocea nodosa* the rate of lateral extension increased with patch size and shoot number in an exponential manner whereas isolated single shoots survived for several years without developing into patches (Vidondo et al., 1997). Such positive effects of increasing patch size are probably linked to reduction of water movement and increased sediment stabilization as patches grow in size (Fonseca et al., 1983). Moreover, the gradual formation of physiologically integrated shoot systems through clonal growth enhances the potential translocation of resources from older shoots on the rhizomes to the apical shoots at the patch edge (Terrados et al., 1997). Such a growth pattern has not, however, been found for *Zostera marina* (Olesen and Sand-Jensen, 1994b) or for *Z. novazelandica* (Ramage and Schiel, 1999), presumably because of the slower horizontal growth of these species resulting in densely packed patches near edge and relatively high nutrient availability at the study sites.

Whereas patch extension is governed by the capacity for rhizome growth there are no constraints on patch recession or mortality. Net growth of patches can be substantially lower than expected from the potential rhizome growth due to loss processes caused by physical and biological disturbance agents. Hence, sediment reworking by burrowing animals can cause disruption of the patch edge (Philippart, 1994; Townsend and Fonseca, 1998) and the erosion of patches at windward margins represents significant disturbances to inhibit expansion of seagrass patches or to cause recession (Fonseca and Bell, 1998). Restriction of patch expansion by the exposure to high flow velocity and the predominantly growth of patches in the shelter, greatly influence the shape and heterogeneity of patches (Fonseca et al., 1983). Accordingly, patch edges are expected to be highly dynamic as confirmed by the high rates of shoot mortality and recruitment found at patch margin compared to inside the patches (Duarte and Sand-Jensen, 1990b).

Disturbances above a certain magnitude are also a common source of patch mortality and even large meadows can disappear during extreme storm events (e.g. Orth and Moore, 1983; den Hartog, 1987). The mortality risk is size-dependent and patch losses are often confined to the smaller patches below a certain threshold size, presumably defined by the species involved and the disturbance regime within the study area (Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vivondo et al., 1997; Ramage and Schiel, 1999). These negative effects of size are probably linked to lack of mutual protection and firm anchorage leading to higher susceptibility to physical disturbances and nutrient stress in small patches. Consequently, patch formation from seeds is typically very inefficient due to high seed and seedling mortality and often less than 10% of newly established seedlings survive past their first year (Churchill, 1983; Duarte and Sand-Jensen, 1990a; Harrison, 1993; Kaldy and Dunton, 1999), although higher survival probabilities have been reported in some populations of *Zostera marina* (24%, Olesen and Sand-Jensen, 1994b) and for *Enhalus acoroides*, and *Thalassia hemprichii* (19 and 22%, Olesen et al., in press). Moreover, the probability of newly established patches to reach a large size is low, as small patches are subject to rapid turnover, as indicated by positively skewed patch size distribution that is frequently found in patchy seagrass stands (e.g. Vidondo et al., 1997). The production of sexual and vegetative propagules remains the term that serves to maintain the positive side of patch dynamics = patch production – thereby ensuring the recovery and formation of seagrass meadows.

C. Resulting Patch Dynamics

The spatial and temporal dynamics of seagrass patches is strongly influenced by the magnitude and frequency of physical disturbances in a given area and by the capacity of the species involved to persist and recover from disturbances. Some seagrass populations experience continuous patch extinction and replacement, which maintains the vegetation in a permanent state of colonization and promotes the development of a mosaic of patches of different age and developmental stages (Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997). When in balance, such populations will maintain a dynamic equilibrium with a uniformity of patch distribution in time and space such that an overall landscape equilibrium of patches applies. This has been demonstrated for *Cymodocea nodosa* growing on highly mobile sediments where the time interval between the passage of consecutive sub-aquatic sand dunes allowed a close balance between loss of vegetation caused by erosion and burial and the formation and development of new patches (Marbà and Duarte, 1995).

The dynamic properties of seagrass patch formation and subsequent growth and survival are essential to the recolonization process in denuded areas. The more than 10-fold span across species in rhizome elongation rates and reproductive effort, defining an upper limit for patch formation from seed, suggests contrasting capacities to recover from disturbances (Duarte et al., 1997b; Marbà and Duarte, 1998; Marbà and Walker, 1999). Small seagrass species exhibit potential fast patch growth, and clonal growth of these species is held responsible for much of the temporal dynamics observed following small-scale disturbances (Williams, 1990; Duarte et al., 1997b). Sexual reproduction is, however, still essential for the recovery of small seagrasses (e.g. Kenworthy, 2000). Nevertheless, some of the larger seagrass species (e.g. *Zostera marina*) with slow elongation rates can achieve high colonization potential by having high reproductive effort (Verhagen and Nienhuis, 1983). In contrast the combination of very slow clonal growth and poor ability to set seeds in other large species (e.g. *Posiodonia oceanica* and *P. sinuosa*) suggests that these are to slow patch growth and an extremely slow recovery process (Duarte, 1995).

Small seagrass species also tend to produce more seeds per ground area than large species and have the ability to build up persistent seed banks whereas large species typically produce seed with no or limited dormancy (Kuo and den Hartog, Chapter 3). However, the rate of patch formation from seeds does not necessarily bear a simple relationship to seed production but is also influenced by loss processes acting on seeds and seedlings and by the seed dispersal capacity (Orth et al., Chapter 5). In a recent study (Olesen et al., 2004), the importance of contrasting reproductive strategies to recovery dynamics was studied over 2.5 years on a mixed-species Philippine seagrass meadow by following patch formation, growth, and mortality in a disturbed gap area (1200 m^2). Different species were involved in sexual vs. colonization as the large species *Thalassia hemprichii* and *Enhalus acoroides* with slow clonal growth but relatively high production of large, broadly dispersed seeds were the major contributors to colonization in areas devoid of vegetation. Although seedling turnover was rapid the high frequency of sexual recruitment (*T. hempricii* 0.052–1.31 m^{-2} $year^{-1}$and *E. acoroides* 0.043–0.081 m^{-2} $year^{-1}$) allowed the successful formation and development of new patches and subsequent patch extension through clonal growth. In contrast the small fast-growing species *Cymodocea rotundata* and *Halodule uninervis* with limited seed dispersal ensured rapid clonal extension ($>$1.5 m $year^{-1}$) of surviving patches in areas where disturbances had only removed part of the existing flora. Hence, where species of both strategies are present, the scale of area affected by disturbance and its interaction with the reproductive strategy of the contrasting species is fundamental to the recovery dynamics of seagrass communities.

V. Gap Dynamics

In seagrass species that form extensive meadows, intense but localized disturbances can cause scars in the meadow that are akin to canopy light gaps in forests. Gap dynamics is a key component of seagrass dynamics (Bell et al., 1999), as gaps are produced often through physical and biological (e.g. Nakaoka and Aioi, 1999) disturbances. In such gaps, the death of later-successional, better competitor species through many different mechanisms can provide small gaps that allow space for the recruitment of new individuals into the forest. As there is often an inverse relationship between competitive ability and colonization potential, the first colonizers to these gaps are generally species that will, through time, be replaced by the original superior competitor (see Pickett and White, 1985 for a detailed treatment of forest light gaps). In *Thalassia*-dominated seagrass beds of the tropical Western Atlantic, small scale physical disturbances caused by wave action or herbivory can remove the dense *Thalassia* canopy and provide room for calcareous macroalgae and faster-growing seagrasses like *Halodule wrightii and Syringodium filiforme* to become established (e.g. den Hartog, 1971; Patriquin, 1973; van Tussenbroek et al., Chapter 18). These features tend to erode at one end and fill in at the other, thereby slowly moving through space in a direction determined by the predominant wave and current regime. At the trailing edge of these 'blowouts', the rapidly colonizing species are replaced by *Thalassia testudinum*, as new ground for the early successional species is cleared at the leading edge by continued erosion. Disturbances like this allow for the coexistence of competitively inferior species in a landscape dominated by a superior competitor. The blowouts in seagrass meadows are very similar to the wind-induced migrating wind-throws responsible for the 'wave-regenerated' evergreen high-latitude forests, in which gaps in the forest generated move slowly upwind at a rate of 1–3 m year^{-1} as old trees succumb to wind fall and younger trees recruit into the space cleared by the wind falls (e.g. Cooper, 1913; Sprugel, 1976). As gap formation and closure are not synchronized in the meadow, a mosaic of different stages of gap dynamics may be encountered in a meadow, maintaining a mosaic of species diversity in the meadow (Duarte et al., 2000). There are, of course, exceptions to this simplified successional pattern, as pioneer species may sometimes develop strategies, such as the formation of a three-dimensional canopy, preventing their exclusion (Fourqurean et al., 1995).

The closure of gaps is primarily dependent on clonal processes, through the extension of rhizomes of the plants at the periphery of the patches onto the gap, as demonstrated by multiple examinations of gap dynamics, including experimental approaches (e.g. Williams, 1987; Rasheed, 1999), as well as observations of recovery of gaps following disturbance, such as those produced by propellers (e.g. Andorfer and Dawes, 2002; Kenworthy et al., 2002).

VI. Dynamics of Seagrass Meadows at Different Time Scales

A. Disturbance

As seagrass meadows provide a variety of ecosystem services, there is much focus on the range and time scales of their variability. At a given site, this variability reflects the frequency and magnitude of disturbances relative to the capacity of the species to resist and recover. Disturbances can be natural or human-induced and are defined here as factors preventing seagrasses from reaching their maximum potential abundance. Natural disturbances most commonly responsible for seagrass loss include extreme climatic events (such as hurricanes) and biological interaction such as diseases, grazing, and bioturbation, while the most common human-induced disturbances are eutrophication, leading to reduced water clarity and quality, and dredging, filling, and certain fishing practices causing direct physical damage (see review by Short and Wyllie-Echeverria, 1996). Changes in light conditions, temperature, and water level, due to climate changes, are also likely to affect the world's seagrass meadows both directly and indirectly and cause large-scale variations, but this aspect is not treated separately here (for further discussion see Walker et al., Chapter 23, and Ralph et al., Chapter 24 and Kenworthy et al., Chapter 25). Tolerance toward disturbances as well as growth and recolonization potentials differ among species and various seagrass species therefore show different temporal and spatial dynamics.

While individual seagrass shoots have a life span of weeks or decades depending on species, meadows, and clones, may in extreme cases persist for centuries or millennia (Reusch et al., 1999; Hemminga and Duarte, 2000). Hence, studies on temporal dynamics of seagrasses tend to focus on different attributes depending on the time scale of interest. Seasonal studies often involve a small spatial scale and focus on attributes such as shoot density or biomass while long-term studies generally involve large spatial scales with focus on population attributes such as presence/absence or area cover. The following sections give examples of changes in abundance of seagrasses on seasonal and interannual time scales and discuss long-term perspectives. For further discussions on landscape dynamics of seagrass meadows, the reader is referred to the chapters by Walker et al., Chapter 23 and Bell et al., Chapter 26.

B. Seasonal Fluctuations

The biomass of seagrasses may change markedly over an annual cycle. A large-scale compilation of data from 14 seagrass species shows that, on average, 70% of the intra-annual variability in biomass of seagrasses reflects seasonal responses (Duarte, 1989). As seasonal variability in seagrass biomass is mainly regulated by changes in light and temperature associated with the solar cycle (Sand-Jensen, 1975; Perez and Romero, 1992; Alcoverro et al., 1995), it changes with latitude. In fact, there seems to be a latitude-dependent upper boundary to seasonal biomass variability rather than a simple linear coupling between the two parameters (Fig. 6; Duarte, 1989). Hence, temperate seagrass communities tend to show greater seasonality but also a wider range of seasonal responses than tropical and subtropical communities, which maintain a more stable biomass throughout the year. However, there is still substantial seasonal variability in some tropical

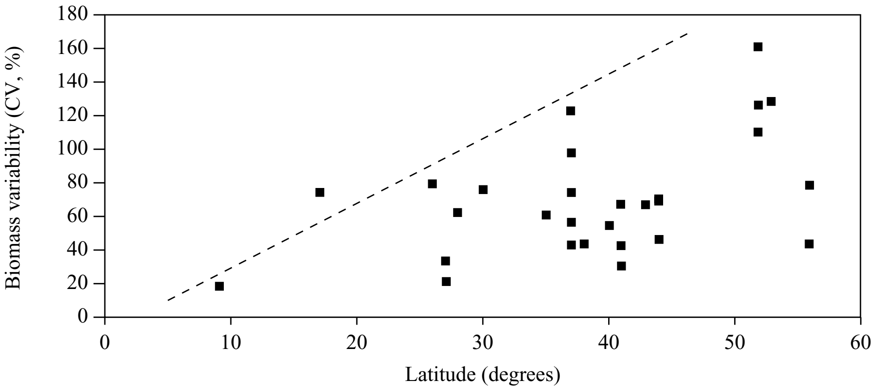


Fig. 6. Relation between the degree of biomass variability (as the coefficient of variation of mean annual biomass), the latitudinal position of seagrasses. Broken line represents the suggested latitude-dependent boundary to biomass seasonality. Data represent 14 different seagrass species. Redrawn from Duarte (1989) with permission.

and subtropical communities. In subtropical south Florida, USA, (ca. 24° N) abundance and growth of *Thalassia testudinum* in summer and winter, respectively, are 30% higher than and 30% lower than the mean even at this relatively low latitude, but the seasonal variability decreases toward the equator and increases toward more northern latitudes (Fourqurean et al., 2001).

The seasonal forcing of light and temperature acts differently on different seagrass species. Growth patterns of the four Western Mediterranean seagrass species (*Cymodocea nodosa, Zostera noltii, Z. marina*, and *Posidonia oceanica*) thus exhibit species-specific differences in the timing and magnitude of seasonal fluctuations even though they experience the same seasonal forcing (Marbà et al., 1996a). These differences may be related to variations in the capacity of plants for storing and allocating resources among ramets. Both processes are positively related to plant size and should enable large seagrass species to grow more independently of environmental conditions than small species (Marbà et al., 1996a). In accordance with these expectations, the largest of the three seagrass species in the Adriatic Sea, *P. oceanica*, shows lower seasonal variation in biomass, shoot density, leaf area index (LAI), shoot weight, and above/belowground biomass than the two smaller species, *Z. marina* and *C. nodosa* (Guidetti et al., 2002). Hence, seasonal forcing seems to be buffered by the availability of internal resources stored in the belowground parts of *P. oceanica* but to be amplified by the lower capacity for storage and allocation in *C. nodosa* and *Z. marina* (Guidetti et al., 2002).

Seasonal variations in temperature may also impose species-specific threshold effects. For instance, the carbon balance of *Zostera marina* becomes negative at high temperature (Marsh et al., 1986) and high temperatures may therefore generate abrupt changes in seasonal growth pattern. At the southern distribution limit of *Zostera marina* in the Gulf of California, USA, where summer water temperatures exceed 25°C, eelgrass thus has an annual life cycle involving growth in winter and dieback in summer (Meling-Lopez and Ibarra-Obando, 1999).

Other seagrass parameters in addition to abundance also show a seasonal pattern that is most likely a direct consequence of the seasonality in carbon balance caused by light and temperature patterns. Growth rate is obviously seasonal, but so are leaf emergence rates (Peterson and Fourqurean, 2001) and flowering and asexual shoot production also show marked seasonal patterns.

C. Inter-Annual and Long-Term Fluctuations

Disturbances, whether natural or human-induced, local or regional, episodic or persistent, may blur the 'natural' seasonal pattern caused by changes in light and temperature and thereby create differences in distribution patterns between years. Whether variations in seagrass populations operate on short or long time scales depends on the intensity and persistence of disturbances, the recolonization potential of the population and the extent of negative feedback effects following the loss of seagrass biomass.

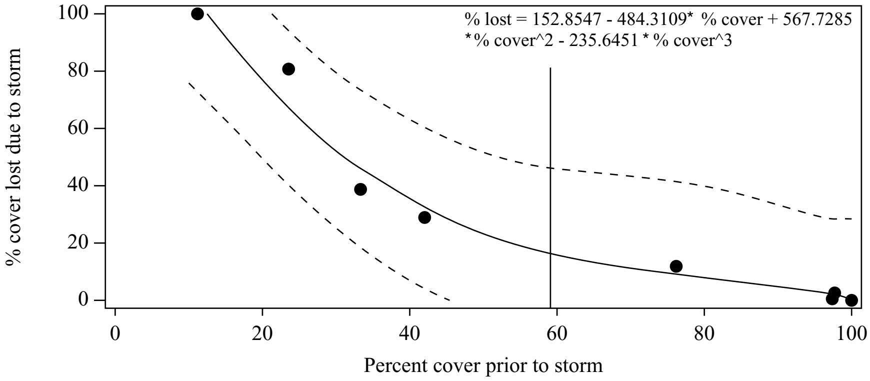


Fig. 7. Percent seagrass cover lost after the March 1993 storm as a function of cover prior to the storm. Vertical line indicates 59% cover (see Fonseca and Bell, 1998) — the theoretical level at which the transition from connected to discontinuous cover takes place. Regression is a cubic fit with 95% confidence limits. Redrawn from Fonseca et al. (2000) with permission.

Physical processes such as wave exposure and tidal currents are among the natural factors that influence the inter-annual variability of seagrass features on both shoot and landscape scales. For example, episodic sediment redistribution by hurricanes is reflected in the growth pattern of *Thalassia testudinum* as changes in length of short shoot internodes (Marbà et al., 1994b), and migrating subaqueous sand dunes induce similar changes in the growth pattern of *Cymodocea nodosa* (Marbà and Duarte, 1994; Marbà et al., 1994a).

On the landscape scale, high exposure and current regimes tend to reduce seagrass cover and increase the fragmentation of seagrass beds (Fonseca and Bell, 1998). A threshold seagrass cover of about 60%, which separates patchy seagrass meadows from large, uniform ones, also separates meadows that suffer structural losses during high-energy periods from those that are more stable (Fonseca and Bell, 1998). Patchy, high-energy beds therefore tend to be more vulnerable to the additional effects of extreme storm events such as hurricanes (Fig. 7; Fonseca et al., 2000). An extreme example of seagrass decline on the landscape scale occurred in Queensland, Australia, when a cyclone and two major floods struck the same area within a period of a few weeks and caused a loss of 1000 km^2 of seagrasses. Shallow populations were uprooted while deep populations died as a result of light deprivation caused by increased water turbidity. After 10 months, no recolonization was detected, but after 2 years marked recolonization from seeds had occurred in deep water (Preen et al., 1995).

As the intensity of physical exposure declines with depth, benthic habitats represent gradients of reduced physical harshness as well as reduced energy input to photosynthesis from shallow to deep water. So with increasing depth, seagrasses experience the contrasting influence of reduced mechanical disturbance, facilitating size development and long-term survival, and reduced light availability, restricting photosynthesis, and plant growth. As a consequence, intermediate water depths often show maximum levels of biomass or cover while shallow waters on wave-swept shores or deep, calm, more shaded waters exhibit reduced biomass (Dring, 1982; Krause-Jensen et al., 2003). In Øresund, Denmark, eelgrass shoot density responds to the vertical gradient by generating many small shoots in the exposed and illuminated shallow waters and fewer but larger shoots with increasing depth (Fig. 8; Krause-Jensen et al., 2000), and these differences create a higher inter-annual variability in shoot density in the shallow-water meadows as compared to the deep-water meadows (Middelboe et al., 2003).

While such patterns toward a greater variability of shallow, compared to deep stands hold within a species, deep seagrass meadows can exhibit intense dynamics whenever formed by fast-growing species. Indeed, *Halophila* species often produce extensive, sparse meadows toward the depth limits to tropical and subtropical stands (e.g. Josselyn et al., 1986; Williams, 1988. These deep stands also experience intense dynamics, due to both intrinsic factors, such as the annual life strategy and rapid rhizome growth of some of these small, fast-growing

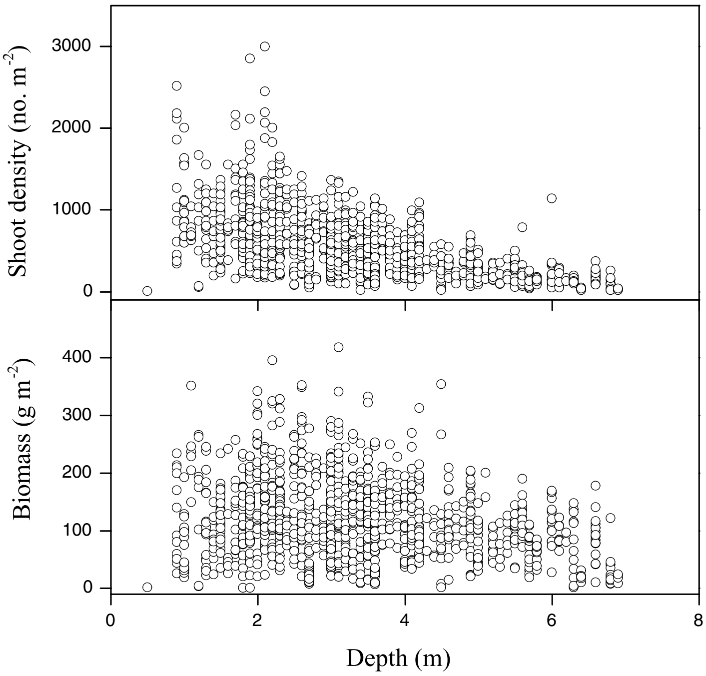


Fig. 8. Eelgrass shoot density (upper panel) and biomass (lower panel) as functions of water depth in Øresund, Denmark. Redrawn from Krause-Jensen et al. (2000) with permission.

species combined with extreme disturbances, such as severe storms and hurricanes reaching down to those depths (e.g. Williams, 1988; Kendall et al., 2004).

Diseases are another category of natural disturbance that may markedly affect the distribution of seagrasses. The world-wide wasting disease that struck *Zostera marina* in the 1930s is the most notable natural event causing long-term and large-scale decline in seagrass communities (Rasmussen, 1977; Short and Wyllie-Echeverria, 1996). Many populations, especially along the Atlantic coasts of Europe, the USA and Canada were completely eradicated (Muehlstein, 1989). The causative agent of the disease is thought to be the slime mould *Labyrinthula* sp. which has also more recently caused diseases to occur locally (e.g. Short et al., 1987; Moore et al., Chapter 16).

Information on recolonization after the eelgrass wasting disease in the 1930s is scattered and mostly qualitative but indicates that large meadows were reestablished during the 1950s and 1960s (Rasmussen, 1977). A recent study based on aerial photos from the period 1940s–1990s shows that shallow Danish eelgrass meadows subjected to the wasting disease exhibited a time lag of more than 10 years before substantial recolonization began, probably reflecting long distances to seed-producing populations and extreme climatic events during that period. After the initial time lag, the eelgrass area increased rapidly and large recoveries had taken place in the 1960s (Fig. 9; Frederiksen et al., 2004). This time scale of 30–40 years corresponds well with model predictions of *Zostera marina* recolonization (Duarte, 1995). However, the distribution area of Danish eelgrass meadows still constitutes only about 25% of the area found around 1900 (Petersen, 1914; Boström et al., 2003). Increased coastal erosion in the period without eelgrass may have made some of the shallow habitats less suitable for eelgrass growth (Rasmussen, 1977) and thereby created a negative feedback loop of seagrass decline. Moreover, reduced water clarity has markedly reduced the potential vertical distribution range as compared to around 1900 (Ostenfeld, 1908; Boström et al., 2003).

Although only few types of herbivores graze directly on seagrasses, grazing may be yet another natural factor regulating seagrass meadows on both small and large scales, especially in subtropical and tropical regions. In the Mombassa Lagoon, Kenya, sea urchin grazing controls the density of the slow-growing seagrass *Thalassodendron ciliatum*

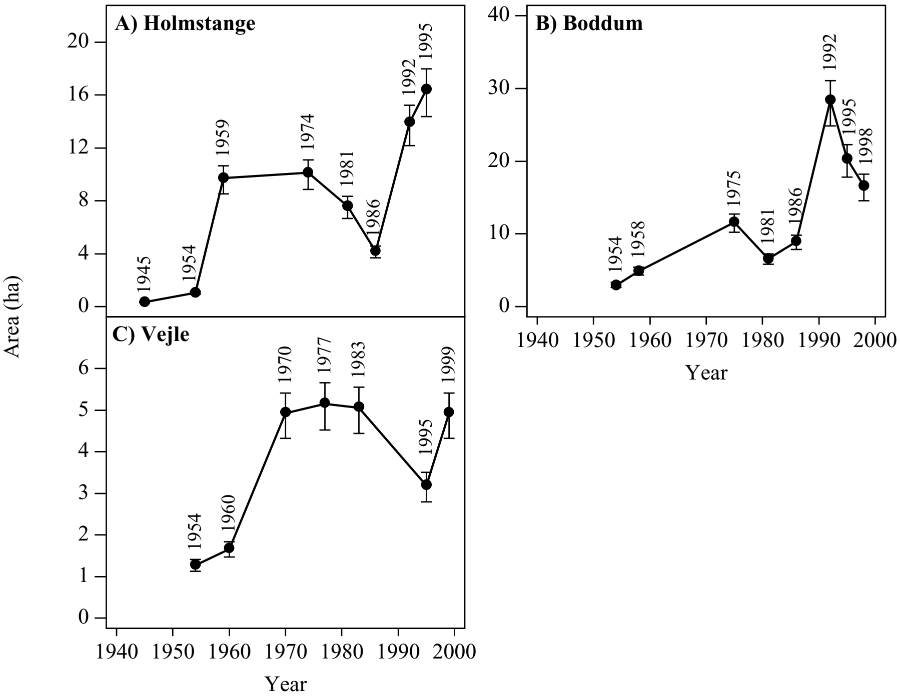


Fig. 9. Long-term changes in eelgrass area distribution at 3 sites subjected to the wasting disease in the 1930s. Eelgrass area distribution was assessed from aerial photos and digital image analysis. Error bars indicate maximum error of interpretation and represent the range between the minimum and the maximum estimate of seagrass cover as evaluated through digital image analysis. Redrawn from Frederiksen et al. (2004) with permission.

and thereby contributes to generating a patchy seagrass landscape with mixed meadows. An example from the outer Florida Bay and the Florida Keys shows that unusually dense populations of sea urchin (>300 individuals m^{-2}) overgrazed and completely denuded a population of *Syringodium filiforme.* The large-scale loss of seagrass biomass initiated community-wide cascading effects that altered resource regimes and species diversity. The loss of seagrass canopy and subsequent death and decay of the belowground biomass destabilized the sediments. As the sediments eroded, turbidity significantly increased, reducing light availability and significantly reducing the sediment nutrient pool and depleting the sediment bank of *S. syringodium* seeds (Rose et al., 1999; Peterson et al., 2002). Explosions in populations of herbivores, such as sea urchins, have been reported from many ecosystems and may be the result of the removal of apex predators by fishing (Jackson et al., 2001).

Seagrasses also constitute the primary food for endangered grazers such as turtles and sea cows, and these giant grazers may introduce marked fluctuations in the biomass and structure of seagrass meadows. In Moreton Bay, Australia, dugongs often graze in large herds at the same location for weeks or months and may thereby reduce the aboveground biomass of seagrasses by up to 96% (Preen, 1995). But following even intense grazing, recovery is usually rapid (months) because the distance between surviving tufts of seagrasses is generally small (<1 m). Grazing may also influence the species composition of seagrass communities, e.g. by favouring pioneer species (Preen, 1995). In fact, the cessation of the plowing of the seafloor by the once abundant grazers must have profoundly altered the ecology of the formerly grazed seagrass beds, and some authors argue that this may have increased the vulnerability of seagrass meadows to recent disturbances (Jackson et al., 2001).

Reduced water clarity caused by increased nutrient inputs or suspended sediments is now the most serious cause of global seagrass decline, and has eradicated several tens of thousands of hectares of seagrass globally (Short and Wyllie-Echeverria, 1996). The newly published World Atlas of Seagrasses provides a global synthesis of the distribution and present status of seagrass meadows and documents that seagrasses are being steadily destroyed by the run-off of nutrients and sediments from land and by boating, land reclamation, dredging, and some fishing methods (Green and Short, 2003). Along with increased eutrophication, negative cascading effects upon the loss of seagrass biomass are common. These involve, for example, increased resuspension of sediments and thereby increased turbidity that further reduces seagrass abundance (Duarte, 1995). Moreover, the occurrence of anoxia during warm calm periods becomes more frequent as eutrophication increases (Rabalais and Turner, 2001) and may seriously affect seagrasses (Terrados et al., 1999; Greve et al., 2003) and cause diebacks (Rask et al., 2000; Plus et al., 2003).

One example of seagrass decline upon increased eutrophication is from the Dutch Wadden Sea. Both the fact that littoral eelgrass gradually disappeared after the mid-1960s and the fact that sublittoral eelgrass beds failed to recover from the wasting disease have been interpreted as responses to increased turbidity caused by eutrophication (Giesen et al., 1990). Florida Bay also experienced a serious loss of seagrasses over a decade (1984–1994), which was partly due to increased turbidity (Hall et al., 1999) and in Chesapeake Bay losses or *Zostera marina* and *Ruppia maritima* were also related to increased turbidity as a result of eutrophication (Orth and Moore, 1983). In Waquoit Bay, Massachusetts Short and Burdick (1996) related housing development and nitrogen loading to eelgrass habitat loss over the period 1987–1992 (Fig. 10). The effect occurred largely via ground water and resulted in a gradual fragmentation and loss of the meadows.

Examples of recolonization upon reduction of eutrophication are limited. The seagrass cover in Cockburn Sound, Western Australia, was markedly reduced between 1976 and 1981 as a response to eutrophication, but reductions in nutrient loads in the 1980s did not lead to recolonization (Walker et al., Chapter 23). It is likely that alterations in shelf-environments during the period without seagrasses have rendered the area unsuitable for seagrass growth (Kendrick et al., 2002). In contrast, *Posidonia coriaceae* and *Amphibolis griffithii* have recolonized former seagrass areas in Success Bank, Western Australia, at surprizingly high rates involving both vegetative and sexual reproduction (Kendrick et al., 1999; Walker et al., Chapter 23). An extremely rapid eelgrass recolonization was also observed in the Archipelago of Southern Funen, Denmark. This area experienced an 80% reduction in the distribution area of eelgrass following an anoxic event during a warm summer period, but recovered completely within 3 years through a combination of vegetative growth of surviving shoots and germination of seeds (Rask et al., 2000). An even faster recolonization of *Z. marina* after anoxia-induced mortality was observed in the Thau Lagoon, French Mediterannean Sea (Plus et al., 2003).

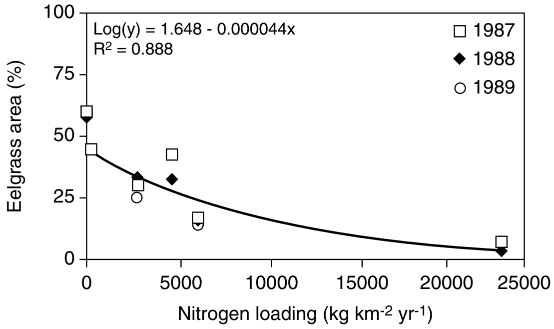


Fig. 10. Comparison of nitrogen loading rates and eelgrass area in the Waquoit Bay estuary's sub-basins over the first three years of study. The log of eelgrass area is regressed against loading. From Short and Burdick (1996), with permission from the Estuarine Research Federation.

Rapid recolonization seems possible if the disturbance causing the seagrass decline is limited in time and space and if seedlings originating from the sediment bank or from neighbouring populations experience suitable growth conditions the following year. By contrast, recovery of seagrass populations from catastrophic decline on the landscape scale requires patch initiation from seeds transported from distant populations and subsequent patch growth. The survival chances of these initial patch stages are low, and the formation of new extended patches may, therefore, be a protracted process. Simulation models show that small species with large recolonization potentials may recover within a few years after a disturbance, while large species with small recolonization potentials may require centuries to recover if the process is at all reversible (Duarte, 1995). Colonization may be further delayed or impeded by negative cascading effects (Duarte, 1995).

In many cases, declines of seagrass meadows are not detected before marked losses have occurred either because surveys have been lacking or methods have been inefficient. Recording of depth limits is a relatively simple way of detecting declines in seagrass populations and as turbidity-related reductions in seagrass cover often affect the deep-water meadows most markedly, the method should be relatively sensitive (see also predictive models based on underwater light fields, discussed in Zimmerman, Chapter 13). Methods involving measurements of population change based on rates of shoot recruitment and mortality have also proved sensitive and may allow early alerts (Duarte et al., 1994; Peterson and Fourqurean, 2001). A large-scale study of the Mediterranean climax species *Posidonia oceanica* thus showed that shoot recruitment does not balance shoot mortality, and the study predicted that shoot density will decline by 50% within 2–24 years if the present disturbance and rate of decline persist (Marbà and Duarte, 1997). These perspectives are serious, especially because meadows of *P. oceanica* represent a very old ecosystem dating back more than 6,000 years, and slow growth rates imply that recolonization may take centuries if the process is reversible at all (Duarte, 1995; Marbà et al., 2002).

VII. Prospect: Forecasting Seagrass Dynamics

The recent declines in seagrass populations worldwide (Green and Short, 2003; Walker et al., Chapter 23; Kenworthy et al., Chapter 25; Ralph et al., Chapter 24) accentuates the need for protecting these valuable ecosystems. As anthropogenic inputs to the coastal zone are the primary cause of the declines (Short and Wyllie-Echeverria, 1996), measures should be taken to reduce these inputs. The many examples of negative cascading effects upon the loss of seagrass biomass emphasize the need for taking action at an early stage.

Moreover, the accumulated knowledge on the mechanism of change and the dynamics in seagrass meadows should be formalized in models forecasting the dynamics of seagrass meadows, and their recovery times. Such models should include predictions of the closure of gaps within meadows. These forecasts are increasingly demanded by managers and our capacity to deliver them is still meagre. Much progress has been made in understanding the dynamics of seagrass meadows since the earlier accounts (den Hartog, 1971). However, although reliable models of clonal growth are now being developed, the prediction of recolonization rates at the landscape scale is problematical (cf. Bell et al., Chapter 26), as the contingencies of patch formation by sexual propagules or vegetative fragments dispersed into an the area is essentially non-predictable. Rare events of long-range dispersal of seeds or vegetative fragments, which cannot be predicted, may play a pivotal role in the recolonization of areas away from any adjacent seagrass source (cf. Orth et al., Chapter 5). Indeed, current knowledge also indicates that the expectation that knowledge on rhizome extension and patch initiation could suffice to predict seagrass dynamics, by upscaling these processes to the landscape scale (e.g. Duarte, 1995), is unsupported, as evidence emerges of increasingly complex dynamics at greater spatial scales (e.g. Sintes et al., 2005; Kendrick et al., 2005).

However, the combined knowledge on seagrass reproduction and dispersal (e.g. Orth et al., Chapter 5), and clonal growth, reviewed above, now allows predictions on the recolonization time scales inherent for different species, which range from one or a few years for the fastest growing species, to several centuries for the slowest-growing ones. As yet, this knowledge has not been formalized into in models delivering, predicted seagrass dynamics under plausible scenarios of growth and new patch initiation.

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Chapter 12

Aquatic Optics: Basic Concepts for Understanding How Light Affects Seagrasses and Makes them Measurable from Space

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I. Introduction

This chapter provides an overview of aquatic optics as it pertains to the transmission of light through the water column and as it impinges on and reflects from benthic substrates, such as seagrasses. This chapter is meant as a primer for Chapter 13 (Zimmerman: Light and Photosynthesis in Seagrass Meadows) and Chapter 15 (Dekker et al., Remote Sensing of Seagrasses). Application of the theory presented here will be developed further in those chapters.

Light transmitted through the atmosphere is modified by absorption and scattering before it hits the surface of the water, where it is either specularly reflected or transmitted across the air–water interface (Fig. 1). The water and its constituents further modify light entering the water, again through processes of absorption and scattering, but also fluorescence and Raman scattering, before it reaches the submerged plant canopy. Thus, it is this modified signal that is of prime importance for photosynthesis of the seagrass meadows, macro-algal beds, coral reefs, and benthic micro-algal mats. This modified signal is also further modified by interactions with the benthic substrate, thus, creating the target signal for remote sensing of optically shallow waters. Before the reflected light reaches the sensor, however, it has to travel back through the water column, the air–water interface and the atmosphere to reach the sensor. Thus, our understanding of submarine photosynthesis and remote sensing of optically shallow environments depends critically on the fundamental principles of hydrologic optics.

II. A Primer on Hydrologic Optics

A. The Radiation Field

The fundamental properties describing the radiation field are defined in precise physical terms, but their symbolic notations in the literature are far from universal. To minimize confusion and to adhere to the increasingly popular conventions emerging from the field of hydrologic optics, the symbols and definitions used here (Table 1) will conform to those of Kirk (1994) and Mobley (1994). The reader is encouraged to consult these excellent texts for a significantly deeper understanding of the fundamental concepts of hydrologic optics introduced here. Although values for the terms and functions defined below are spectrally dependent, the parenthetical notation (λ) has been omitted from the equations for simplicity. Direction within the light field is generally expressed in terms of the zenith, nadir, and

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A. W. D. Larkum et al. (eds.), Seagrasses: Biology, Ecology and Conservation, pp. 295–301.

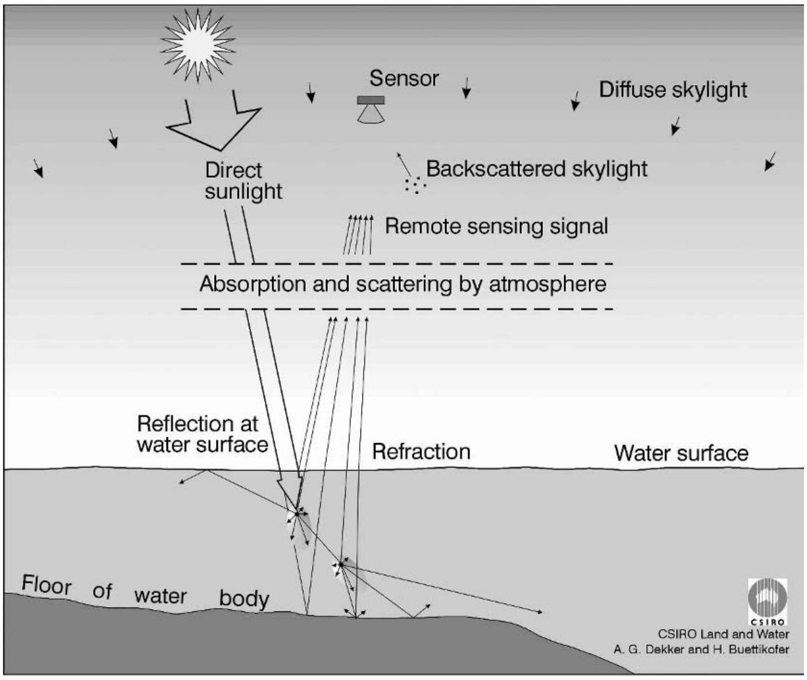

Fig. 1. A schematic diagram of the various processes that contribute to the signal as measured by a remote sensor in optically shallow water where the substrate has a significant effect on the water-leaving radiance (source: Dekker et al., 2001).

azimuth angles (θ, θ_n, and ϕ, respectively) as illustrated in Fig. 2.

The *radiant flux* represents the time rate of flow of radiant energy, and is denoted by the symbol Φ. Radiant flux can also be expressed in molar units, where 1 mol $= 6.02 \times 10^{23}$ photons (Avogadro's number). According to Kirk (1994), terms such as 'fluence rate' or 'photon fluence rate' should be avoided when describing properties of the radiation field. The *field radiance* (L) is the radiant flux projected onto a surface dA oriented at right angles to the incident beam (Fig. 2) and has units of W (or quanta s^{-1}) m^{-2} steradian^{-1}. The *surface radiance* is the radiant flux in a given direction per unit solid angle projected onto a horizontal surface (dS) oriented at some angle (θ, ϕ) to the beam. It is denoted by the symbol L (θ, ϕ) and also has units of W (or quanta s^{-1}) m^{-2} steradian^{-1}. The surface radiance is related to the field radiance according to the Cosine Law because the horizontal surface area (dS) is defined by $\frac{\mathrm{d}A}{\cos\theta}$.

Irradiance is the total radiant flux incident upon a surface of defined area. It is denoted by E, and has units of W (or quanta s^{-1}) m^{-2}. The scalar irradiance (E_o) integrates the radiance distribution equally over all directions of a sphere:

$$E_o = \int_{4\pi} L(\theta, \phi)\mathrm{d}\omega \tag{1}$$

Scalar irradiance can be partitioned into downward and upward scalar irradiances, but it will be more useful to consider downward and upward *plane* irradiances in the discussion of seagrass–light interactions found in Chapter 13. The downward and upward plane irradiances (E_d and E_u) illuminate the upper and lower faces of a surface, respectively. Like scalar irradiances, they are obtained by integrating the radiance over all solid angles (ω) of the upper and lower hemispheres, separately. Unlike scalar irradiances, however, plane irradiances are affected by the Cosine Law, which simply states that the irradiance incident on a plane surface is proportional to the angle between the photon direction and the surface normal (Fig. 2). Hence:

$$E_d = \int_{2\pi} L(\theta, \phi) \cos\theta \mathrm{d}\omega \tag{2}$$

Abbreviations: See Table 1 for a list of symbols, definitions, and units used in this chapter.

Table 1. Symbols, definitions, and units of some common terms used in hydrologic optics.

Symbol	Definition	Dimensions
Fundamental quantities		
ϕ	Azimuth angle	deg or rad
θ	Polar angle	deg or rad
θ_n	Zenith polar angle	deg or rad
θ_n	Nadir polar angle	deg or rad
μ	Cosine of polar angle	Dimensionless
Z	Depth	m
Radiometric quantities		
L	Radiance	W (or quanta s^{-1}) m^{-2} sr^{-1} nm^{-1}
L_u	Upwelling radiance	W (or quanta s^{-1}) m^{-2} sr^{-1} nm^{-1}
L_w	Water-leaving radiance	W (or quanta s^{-1}) m^{-2} sr^{-1} nm^{-1}
E	Irradiance	W (or quanta s^{-1}) m^{-2} nm^{-1}
E_0	Scalar irradiance	W (or quanta s^{-1}) m^{-2} nm^{-1}
E_d	Downwelling plane irradiance	W (or quanta s^{-1}) m^{-2} nm^{-1}
E_u	Upwelling plane irradiance	W (or quanta s^{-1}) m^{-2} nm^{-1}
Inherent optical properties		
A	Beam absorptance	Dimensionless
B	Beam scatterance	Dimensionless
T	Beam transmittance	Dimensionless
D	Optical density	Dimensionless
a	Beam absorption coefficient	m^{-1}
b	Beam scattering coefficient	m^{-1}
c	Beam attenuation coefficient	m^{-1}
β	Volume scattering function	m^{-1} sr^{-1}
Apparent optical properties		
R	Irradiance reflectance	Dimensionless
R_{rs}	Remote sensing reflectance	sr^{-1}
K_d	Coefficient of downwelling attenuation	m^{-1}
K_u	Coefficient of upwelling attenuation	m^{-1}
$\bar{\mu}_d$	Average cosine of downwelling irradiance	Dimensionless
$\bar{\mu}_u$	Average cosine of upwelling irradiance	Dimensionless

Similarly, the upward plane irradiance is obtained by integrating the radiance over all solid angles of the lower hemisphere, with respect to the Cosine Law:

$$E_u = \int\limits_{-2\pi} L(\theta_n, \phi) \cos \theta_n d\omega \tag{3}$$

Application of the Cosine Law means that E_o is always greater than the sum $(E_d + E_u)$.

B. Inherent and Apparent Optical Properties

The bulk properties of natural waters are often divided into *inherent* and *apparent* optical properties, respectively. Inherent optical properties (IOPs) include the beam absorption, beam scattering, and beam attenuation coefficients (a, b, and c, respectively). By definition, IOPs depend only upon the medium, including its dissolved and suspended components. The geometry or magnitude of the incident light field does not influence them. Apparent optical properties (AOPs) also are determined by the medium, but additionally are influenced by the geometry and magnitude of the incident light field because they are based on irradiances, rather than field radiances. Apparent optical properties include irradiance reflectance (R), remote sensing reflectance (R_{rs}), and the coefficients of vertical light attenuation (K-functions). When we divide E_u by E_d we obtain the irradiance reflectance at the point of measurement, which is important for remote sensing purposes. The coefficient of vertical light attenuation defines the relative loss of light with increasing depth.

C. Inherent Optical Properties

Consider a beam of light incident on a small volume ΔV of medium (e.g. water or a plant leaf) with a thickness Δr (Fig. 3). Some of the beam's radiant

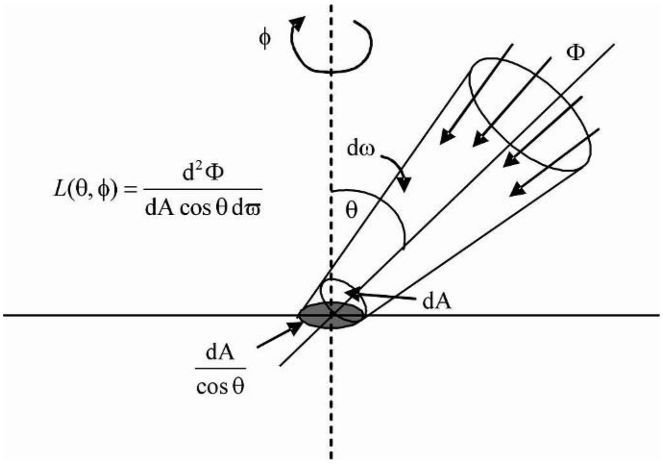

Fig. 2. Definitions of radiance and angular orientation at a point in space (after Kirk, 1994). $L(\theta, \phi)$ is the radiance incident on area dA at zenith angle θ and azimuth angle ϕ, given the radiant flux Φ into the small solid angle dω. The Cosine Law is illustrated by the relationship between the area of illumination normal to dω, defined by dA, and the surface-normalized area of illumination, $\frac{dA}{\cos\theta}$.

flux is absorbed within the medium (Φ_a), some is scattered out of the beam (Φ_s), and some is transmitted unaltered through the medium (Φ_t). The beam absorptance (A) represents the fraction of the incident radiant flux absorbed by the medium:

$$A \equiv \frac{\Phi_a}{\Phi_i} \tag{4}$$

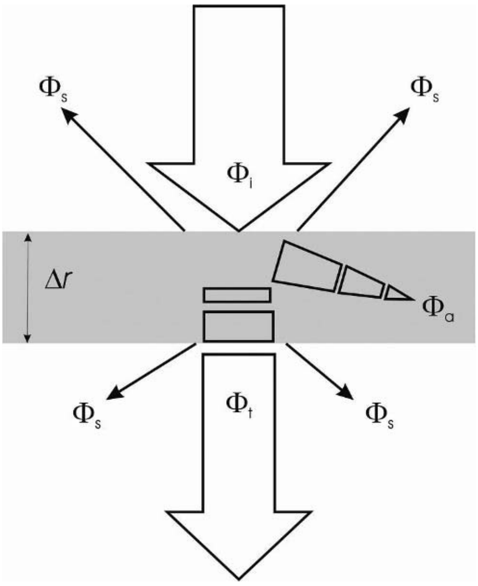

Fig. 3. Interaction of a beam of light with a thin optically active layer. The flux incident (Φ_i) on the medium of thickness Δr is dissipated by scattering out of the path (Φ_s) and by absorption (Φ_a) within the medium. The remaining flux (Φ_t) is transmitted out of the medium.

The beam scatterance (B) is the fraction of incident radiant flux scattered out of the beam:

$$B \equiv \frac{\Phi_s}{\Phi_i} \tag{5}$$

Finally, the beam transmittance (T) is the fraction emerging from the medium:

$$T \equiv \frac{\Phi_t}{\Phi_i} \tag{6}$$

It thus follows that $A + B + T = 1$ because these terms represent dimensionless ratios normalized to the incident flux. In hydrologic optics, the absorption and scattering coefficients have dimensions of inverse meters (i.e. m^{-1}). Thus, the beam absorption and scattering coefficients are defined as the depth derivatives of the absorptance and scatterance over an infinitesimally small distance (Δr):

$$a \equiv \lim_{\Delta r \to 0} \frac{A}{\Delta r} \tag{7}$$

$$b \equiv \lim_{\Delta r \to 0} \frac{B}{\Delta r} \tag{8}$$

Beam attenuation is defined by summing the absorption and scattering coefficients:

$$c \equiv a + b \tag{9}$$

If we assume $B = 0$, as in the case of a transparent chemical solution subjected to spectrophotometric analysis, the transmittance represents the fraction of incident light that was not absorbed. In that case, the absorbance, or optical density, is defined as:

$$D \equiv \log_{10} \frac{\Phi_i}{\Phi_t} \tag{10}$$

It follows that:

$$A = 1 - 10^{-D} \tag{11}$$

Unlike the transparent solution mentioned above, however, scattering has a major impact on the fate and distribution of light in natural waters. Scattering impedes vertical light penetration by prolonging the path length, which increases the probability of absorption. Scattering also propagates photons back into the direction of the downwelling light. Earth observation sensors measure the backscattered photons that survive the water column, the air–water interface and the atmosphere. In most cases, the aim of applying earth observation is to reconstruct the constituents causing that backscattering.

The way in which scattering affects the penetration of light into the medium depends on the angular distribution of the scattered flux. This angular distribution has a characteristic shape for any given medium and is specified in terms of the normalised volume scattering function (β). The scattering coefficient b can be obtained by integration of β over all directions (solid angles). The measurement of β, however, is not trivial and b is routinely calculated (not measured) from easier-to-obtain measurements of beam absorption and attenuation ($b = c - a$).

It is important to distinguish between forward vs. downward scattering and upward vs. backward scattering. These pairs are identical only for vertically incident light (sun at zenith of 0°) and a flat water surface. As soon as we deviate from these circumstance forward and backward scattering describe the scattering processes with respect to the angle of the incident light (which may be e.g. sunlight at 10, 20, ... 80° from zenith) whereas upward and downward scattering describe the fractions of incident light (at any incident angle) that are scattered relative to the surface normal (Fig. 4). Although the mathematics are significantly more complicated for scattering than for absorption, their bulk effects on light attenuation in natural waters are often summarized by the average cosine ($\bar{\mu}$), an apparent optical property discussed below.

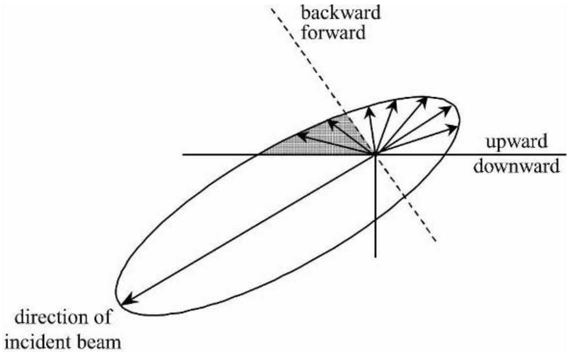

Fig. 4. Definitions of scattering direction. Forward and backward scattering are defined relative to the direction of the incident beam. Downward and upward scattering are defined relative to a horizontal surface. Thus, the upwelling light detected by remote sensing is derived from light scattered in both forward and backward directions.

The volume scattering function describes an elastic process in which the scattered photon has the same wavelength and polarization as the incident photon. Inelastic scattering, by contrast, implies a change in the wavelength and/or polarization of the scattered photon. Raman scattering and fluorescence represent two types of inelastic scattering that may be relevant in natural waters. Both processes cause a shift to longer wavelengths. Raman scattering, however, is virtually instantaneous. Although it involves some transfer of energy from the photon to the target molecule (hence the wavelength shift), the scattered photon retains its characteristic incident polarization. Raman scattering in natural waters results primarily from photon interactions with water molecules, which makes it a relatively constant factor that influences the underwater light slightly between 550 and 650 nm. Fluorescence is an absorption–emission process that requires at least 10^{-9} s (a long time in the particle physics world) and the emitted photon is unpolarized with respect to the incident photon. Fluorescent substances in natural waters include dissolved organic matter and photosynthetic pigments contained in phytoplankton, seagrasses, macrophytes, and symbiotic algae. Typically 1–5% of the photosynthetically absorbed photons are emitted by chlorophyll as fluorescence in a 25 nm band centered at 685 nm (Falkowski and Raven, 1997).

D. Apparent Optical Properties

Apparent optical properties (AOPs) are derived from the IOPs defining the medium, combined with the angular distribution of the ambient light field. As such, AOPs will be affected by the time of day, degree of cloud cover, sea surface state and depth within the water column. The most commonly used AOPs are the diffuse attenuation coefficients or "K" functions. K functions, also referred to as quasi-inherent optical properties, because the effects of changes in the incident radiation field are generally small, although that is not always the case (Baker and Smith, 1979, but see Miller and McPherson, 1995). Because the irradiance within a sunlit + skylit water body decreases approximately exponentially with depth, it is conventional to describe that relationship using the Lambert-Beer equation. Thus, the downwelling plane irradiance anywhere within the water column [i.e. $E_\mathrm{d}(z)$] is a function of the in-water irradiance at the surface [$E_\mathrm{d}(0)$], the diffuse attenuation coefficient for downwelling irradiance (K_d), and the depth (z) of the overlying water column:

$$E_\mathrm{d}(z) = E_\mathrm{d}(0)\exp(-K_\mathrm{d}z) \tag{12}$$

Solving for K_d yields:

$$K_\mathrm{d} = \frac{-\ln\left[\frac{E_\mathrm{d}(z)}{E_\mathrm{d}(0)}\right]}{z} \tag{13}$$

Thus, the diffuse attenuation coefficient is easily approximated from vertical profiles of *spectral* irradiance. The diffuse attenuation coefficients for upwelling plane irradiance and scalar irradiance are defined by similar equations. K functions of broadband irradiance (e.g. PAR) provide convenient, albeit much less perfect, descriptors of light attenuation because they do not properly account for the strong wavelength-dependency of absorption. This can be an especially significant problem for estimating light availability for seagrass photosynthesis in green coastal waters (see Chapter 13). The K-functions are dimensionalized with the same units (inverse length) as the IOPs, but it is important to remember that the IOPs refer to the loss of radiant power from a collimated beam. K functions represent the attenuation of naturally diffuse light comprised of photons traveling in all directions.

The average cosine $\bar{\mu}$, another AOP, provides a useful way to approximate the angular structure of the submarine light field in terms of a single parameter. For a collimated beam oriented at angle (θ) relative to the zenith, $\bar{\mu}_\mathrm{d} = \cos\theta$. Thus, the average pathlength of photons traveling downward through the water, and therefore the magnitude of the diffuse attenuation coefficient, is proportional to $\frac{1}{\bar{\mu}_\mathrm{d}}$. The downwelling average cosine can also be calculated from the ratio of the downwelling plane irradiance normalized to the downwelling scalar irradiance:

$$\bar{\mu}_\mathrm{d}(z) \equiv \frac{E_\mathrm{d}(z)}{E_\mathrm{od}(z)} \tag{14}$$

The upwelling average cosine is defined similarly as:

$$\bar{\mu}_\mathrm{u}(z) \equiv \frac{E_\mathrm{u}(z)}{E_\mathrm{ou}(z)} \tag{15}$$

Values of $\bar{\mu}_\mathrm{d}$ typically range from 0.9 to 0.75 in natural waters. A typical value for $\bar{\mu}_\mathrm{u}$ is about 0.39. If the light field is isotropic (i.e. equal intensity in all directions), $\bar{\mu}_\mathrm{d} = \bar{\mu}_\mathrm{u} = 0.5$.

III. Radiative Transfer in Natural Waters

Radiative transfer theory provides a macroscopic, linear approximation for calculating the loss of radiant energy of a beam due to absorption and scattering along a defined path, and the gain of energy by scattering into the path. As such, it creates a robust framework to develop mechanistic models of the submarine light environment, system-level productivity and remotely sensed reflectance of seagrass meadows in optically shallow waters. Exact solutions to the radiance transfer equations have been developed for natural waters in which the optical medium is a continuous material composed of randomly arranged scattering elements separated by large distances relative to the wavelength of light (Mobley, 1994). Plant leaves, however, represent a dense packaging of optically active material, which violates the single-scattering assumptions of these exact solutions. Consequently, models of irradiance distribution in submerged plant canopies must rely on more empirical relationships between leaf optical properties and light attenuation by the bulk canopy as well as the water column (Goudriaan, 1988; Shultis and Myneni, 1988; Ganapol and Myneni, 1992; Zimmerman, 2003).

Chapter 13 will consider the development of such models for submerged plant canopies and the implications for leaf photosynthesis, ecosystem level productivity. Chapter 15 will discuss how IOPs, AOPs, and radiative transfer theory can be used to develop quantitative methods for remote sensing of submerged aquatic vegetation.

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Chapter 13

Light and Photosynthesis in Seagrass Meadows

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I. Introduction

The distribution of radiant energy in plant canopies determines one of the fundamental interactions of biophysical ecology—that of energy exchange between photosynthetic organisms and their environment. Accurate knowledge of light absorption by plant canopies permits the calculation of important plant- and ecosystem-level properties, including rates of primary production, which will be the focus of this chapter. Knowledge of the interaction between light and plant canopies is also crucial for remote sensing, quantification of vegetation abundance and distribution, as well as for the development of inversion, techniques to infer plant chemical composition, important for ecosystem-scale estimates of plant growth and biogeochemical fluxes (Jacquemoud et al., 1996; Lacapra et al., 1996; Broge and Leblanc, 2000). Submerged aquatic vegetation, including seagrass beds, provide a strong optical signature that can be tracked using satellite and airborne remote sensing (Armstrong, 1993; Mumby et al., 1997; Chauvaud et al., 2001; Dierssen et al., 2003), and this will be the subject of Dekker et al., Chapter 15.

Seagrasses represent an ecologically important structuring element and major source of primary production in shallow waters, worldwide. The primacy of light availability in determining seagrass bed density, distribution and productivity is particularly acute (Hemminga and Duarte, 2000). Although minimum light requirements for most marine macrophytes are on the order of 0.1 to 1% of in-water surface irradiance [$E_\mathrm{d}(0)$], seagrasses have unusually high light requirements, ranging from 10% to as much as 37% of $E_\mathrm{d}(0)$ (Duarte, 1991b; Olesen and Sand-Jensen, 1993; Kenworthy and Fonseca, 1996). These high light requirements, which can be traced, at least partially, to inefficient carbon-concentrating mechanisms for photosynthesis (Durako, 1993; Beer and Rehnberg, 1997; Zimmerman et al., 1997; Invers et al., 2001; Larkum et al., Chapter 14), make seagrasses particularly vulnerable to deteriorated water quality and light competition from micro- and macroalgal blooms induced by eutrophication (Short and Wyllie-Echeverria, 1996; Ralph et al., Chapter 24). Consequently, the development of robust mechanistic relationships between the submarine light field and photosynthesis of submerged plant canopies will facilitate our fundamental understanding of coastal biogeochemical processes and assist in the management of these important coastal resources.

Light-dependent productivity of seagrass beds has been estimated from photosynthesis vs. irradiance (P vs. E) relationships measured at scales ranging from individual leaves (e.g. Dennison and Alberte, 1982, 1985; Zimmerman et al., 1994; Zimmerman et al., 2001) to individual multi-leaved shoots (Fourqurean and Zieman, 1991) to *in situ* benthic chambers enclosing multiple shoots (Dunton, 1994; Herzka and Dunton, 1997; Mateo et al., Chapter 7). Each approach can provide reasonable local estimates of whole plant photosynthesis, carbon balance and light requirements, which has made this general approach extremely useful for exploring the relationship between environmental forcing and primary productivity in tightly focused local studies. Unfortunately, the functional relationships behind these relatively simple "big leaf" budgets are not readily transported to seagrass beds growing in different light environments because they do not account for the interactions between the overlying water column and the distribution and orientation of the

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plant canopy relative to the incident light field, or to the spectral quality of the incident light. Further, it is difficult to evaluate potentially important density dependent effects (e.g. self-shading) with these "big leaf" models. Finally, the data required to develop and validate the empirical models are time consuming to collect and not easily automated, which limits their utility for resource management objectives.

We can develop a more mechanistic understanding of seagrass bed productivity by employing some biophysical principles and geometric reasoning to characterize the general interaction of seagrass canopies with the submarine light field and water column in which they are embedded. This chapter focuses on the vertical distribution and orientation of leaf biomass (Fig. 3), and the optical properties of leaves that determine spectral light absorption by the plant canopy (Fig. 4) within an optically active water column. An overview of general terms and principles of radiative transfer theory relevant to this discussion is presented in Zimmerman and Dekker, Chapter 12. More detailed treatments of radiative transfer theory applied to natural waters can be found in Kirk (1994) and Mobley (1994).

II. Radiation Transfer and Light Interception

If we ignore scattering and assume leaves to be optically black, then the probability that a photon will be transmitted through a horizontally homogeneous canopy composed of randomly distributed horizontal leaves of unit thickness can be approximated by application of the Lambert-Beer Law of radiative transfer. Mathematically, the transmittance (T) is defined as:

$$T = \frac{\Phi_t}{\Phi_i} = \exp\left(-\frac{L}{\cos\theta}\right) \tag{1}$$

where, Φ_t is the flux transmitted through the canopy, Φ_i represents the radiant flux of a beam incident on the canopy, L is the one-sided leaf area index of the population of randomly distributed horizontal leaves and θ is the zenith angle of the incident beam (Table 1). If the light is directly overhead (i.e. perpendicular to a horizontal surface), $\theta = 0$ and cos $\theta = 1$. Conversely, the absorptance (A), or probability of a photon being absorbed by the canopy is 1 minus the probability of transmission:

$$A = \frac{\Phi_a}{\Phi_i} = 1 - \frac{\Phi_t}{\Phi_i} = 1 - T \tag{2}$$

The leaves of real plant canopies, however, are almost never horizontally oriented, nor randomly distributed, especially in the vertical. And their optical density is neither black nor even spectrally neutral. Additionally, the angular distribution of natural sunlight is composed of both direct and diffuse components, which complicates the estimation of θ. Furthermore, leaves scatter a significant portion of the incident beam in both the forward and backward directions, changing the angular distribution of light as it passes through the canopy. Finally, the natural water column in which seagrass canopies are suspended is also a source of light attenuation and scattering. The development of accurate relationships describing the interaction between submerged plant canopies and the incident light field requires that we account for these complications.

III. Canopy Architecture and Leaf Orientation

The first step in developing a robust theory of seagrass–light interactions requires a mathematical description of the distribution of leaf biomass within the canopy (Fig. 1). For the remainder of this chapter, we will assume that leaf biomass distribution is horizontally homogeneous, allowing us to focus on a one-dimensional (i.e. vertical) problem. The driving physical principles are essentially the same for the three-dimensional problem but the algebra becomes more cumbersome (Norman and Welles, 1983). The following notation will employ the use of parenthetical terms (λ) and/or (z) to denote that the values of some variables depend on wavelength and/or depth within the canopy. All seagrass species bear leaves that emerge more-or-less vertically from the base of a vertical shoot. Most leaves are flat and strap-like, the notable exception being the elliptical petiolated leaves of *Halophila* spp. and the cylindrical leaves of *Syringodium* spp. Nonetheless, the basal origin of the leaves allows the vertical distribution of canopy biomass to be determined from knowledge of the width and the

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Abbreviations: For a list of symbols, definitions, and units see Table 1, Zimmerman and Dekker, Chapter 12.

Table 1. List of model symbols, their definitions and dimensions. Parenthetic notation of λ and z indicates that the quantity is wavelength (λ) and/or depth (z) dependent, respectively.

Symbol	Definition	Dimensions
Fundamental quantities		
T	Daylength	s day^{-1}
θ	Polar angle	deg
μ	Cosine of polar angle	Dimensionless
z	Depth within the canopy	m
Δz	Vertical thickness of canopy layers	m
Canopy architecture properties		
$B(z)$	Biomass fraction in layer z	Dimensionless
β	Nadir bending angle of the seagrass canopy	degrees
h_{m}	Maximum canopy height	m
h_{c}	Realized canopy height	m
$h(z)$	Height above the seabed	m
I	Intermediate height of sigmoid biomass distribution	m
L	Canopy leaf area index	m^2 leaf m^{-2} seabed
L_{s}	Leaf area per shoot	m^2 leaf shoot^{-1}
$l(z)$	Leaf area index at depth z	m^2 leaf m^{-2} seabed
$l_{\mathrm{p}}(z)$	Horizontally projected leaf area at depth z	m^2 leaf m^{-2} seabed
t_{L}	Leaf thickness	m
s	Shape factor for sigmoid biomass distribution	Dimensionless
ψ	Percent of canopy biomass at the seabed	Dimensionless
Radiometric quantities		
$E_{\mathrm{d}}(\lambda, z)$	Downwelling plane irradiance transmitted through layer z	W (or quanta s^{-1}) m^{-2} nm^{-1}
$E_{\mathrm{u}}(\lambda, z)$	Upwelling plane irradiance transmitted through layer z	W (or quanta s^{-1}) m^{-2} nm^{-1}
Φ_{i}	Incident flux	W (or quanta s^{-1})
Φ_{t}	Transmitted flux	W (or quanta s^{-1})
Φ_{a}	Absorbed flux	W (or quanta s^{-1})
Φ_{r}	Reflected flux	W (or quanta s^{-1})
Inherent optical properties		
$a_{\mathrm{L}}(\lambda)$	Leaf absorption coefficient	m^{-1} of leaf thickness
$A_{\mathrm{L}}(\lambda)$	Leaf-specific absorptance	Dimensionless
$D(\lambda)$	Leaf-specific absorbance	Dimensionless
$R_{\mathrm{L}}(\lambda)$	Leaf reflectance	Dimensionless
$R_{\mathrm{b}}(\lambda)$	Seabed reflectance	Dimensionless
$R_{\mathrm{d}}(\lambda, z)$	Canopy reflectance of downwelling irradiance	Dimensionless
$R_{\mathrm{u}}(\lambda, z)$	Canopy reflectance of upwelling irradiance	Dimensionless
Apparent optical properties		
$K_{\mathrm{d}}(\lambda)$	Water column attenuation of downwelling irradiance	m^{-1}
$K_{\mathrm{u}}(\lambda)$	Water column attenuation of upwelling irradiance	m^{-1}
$\bar{\mu}_{\mathrm{d}}(z)$	Average cosine of downwelling irradiance	Dimensionless
$\bar{\mu}_{\mathrm{u}}(z)$	Average cosine of upwelling irradiance	Dimensionless
Photosynthetic properties		
$PUR(z)$	Photosynthetically utilized irradiance in layer z	quanta absorbed m^{-2} leaf s^{-1}
ϕ_{p}	Quantum yield of photosynthesis	Mol C mol^{-1} PUR
$P_{\max}$	Rate of light saturated photosynthesis	Mol C m^{-2} leaf s^{-1}
$P_{\mathrm{i}}(z)$	Biomass-specific photosynthesis in layer z	Mol C m^{-2} leaf s^{-1}
P_{c}	Depth-integrated biomass-specific photosynthesis	Mol C m^{-2} leaf s^{-1}
P_{d}	Daily integrated biomass-specific photosynthesis	Mol C m^{-2} leaf day^{-1}
$\Re$	Metabolic respiratory demand	Mol C m^{-2} leaf day^{-1}

length-frequency distribution of leaves within a population. Most leaves in the population are of intermediate length, but the fact that all leaves emerge from a basal sheath means that the fractional amount of leaf biomass within the canopy is greatest near the seafloor and decreases non-linearly toward the top of the canopy (Fig. 1). This general relationship can be represented by a sigmoid function that

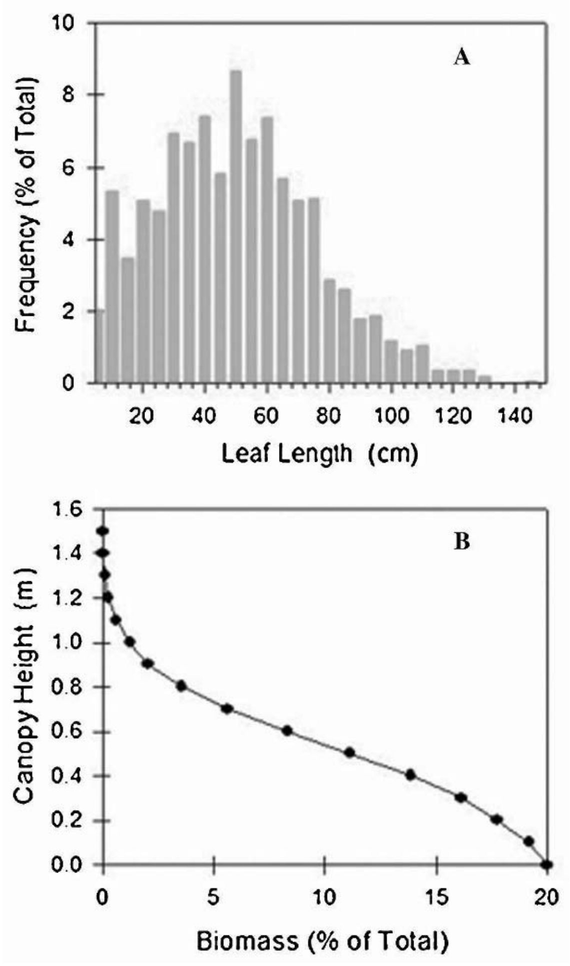

Fig. 1. (A) Length-frequency distribution for a population of eelgrass leaves. (B) Relative vertical distribution of leaf biomass resulting from the size-frequency distribution illustrated in (A).

accurately describes the relative distribution of leaf biomass in seagrass canopies ranging in height from 0.1 to over 1.0 m in height (Zimmerman, 2003). The relative amount of biomass [$B(z)$] at any depth (z) is defined as a function of the percentage of biomass at the base of the canopy (ψ), the height of that point above the seafloor [$h(z)$], an intermediate point within the canopy (I), and a shape factor (s):

$$B(z) = \frac{\psi}{1 + \left[\frac{h(z)}{I}\right]^{s}} \tag{3}$$

The values of ψ, I and s can be easily parameterized in a couple of ways. Iterative non-linear regression can provide precise parameter estimates for specific populations using a known leaf size-frequency distribution. Alas, such data are not always readily available. However, consistent relationships among morphometric characters of seagrasses often transcend the boundaries of individual populations and species (Duarte, 1991a; Terrados et al., 1999). Consequently, the vertical biomass distribution defined by Eq. (3) can be parameterized from a knowledge of canopy height (h_c) alone (Zimmerman, 2003):

$$\psi = 2.51 h_c^{-0.79} \tag{4}$$

$$I = 0.588\,[1 - \exp(-1.12 h_c)] \tag{5}$$

The shape factor (s) is independent of canopy height but turns out to be relatively constant (4.75 ± 0.20 across seagrass canopies ranging from 0.10 to >1 m in height. Furthermore, the total one-sided leaf area per shoot can also be estimated from knowledge of canopy height:

$$L_s = 0.0063 h_c + 0.019 h_c^2 \tag{6}$$

Consequently, computing the absolute vertical distribution of seagrass biomass requires only a knowledge of canopy height and shoot density, since the total leaf area index of the canopy (L) is the product of L_s and shoot density:

$$l(z) = L \cdot B(z) \tag{7}$$

In this case, $l(z)$ represents the leaf area index at depth z within the canopy.

Given a knowledge of the vertical biomass distribution, we next account for the geometric orientation of the leaves relative to the incident light field. Phytoplankton, because of their quasi-spherical shape, respond to the submarine light field as scalar irradiance collectors. Thus the amount of light arriving at the cell surface, and therefore the probability of light absorption by photosynthetic pigments, is independent of cell orientation relative to the incident light field. In other words, the shadow cast by a phytoplankton cell is independent of its orientation with respect to the illuminating beam. The shadow cast by a flat seagrass leaf, however, is strongly dependent on the angular relationship between the leaf and the submarine light field. Consequently, interception of the downwelling irradiance by the canopy in layer z

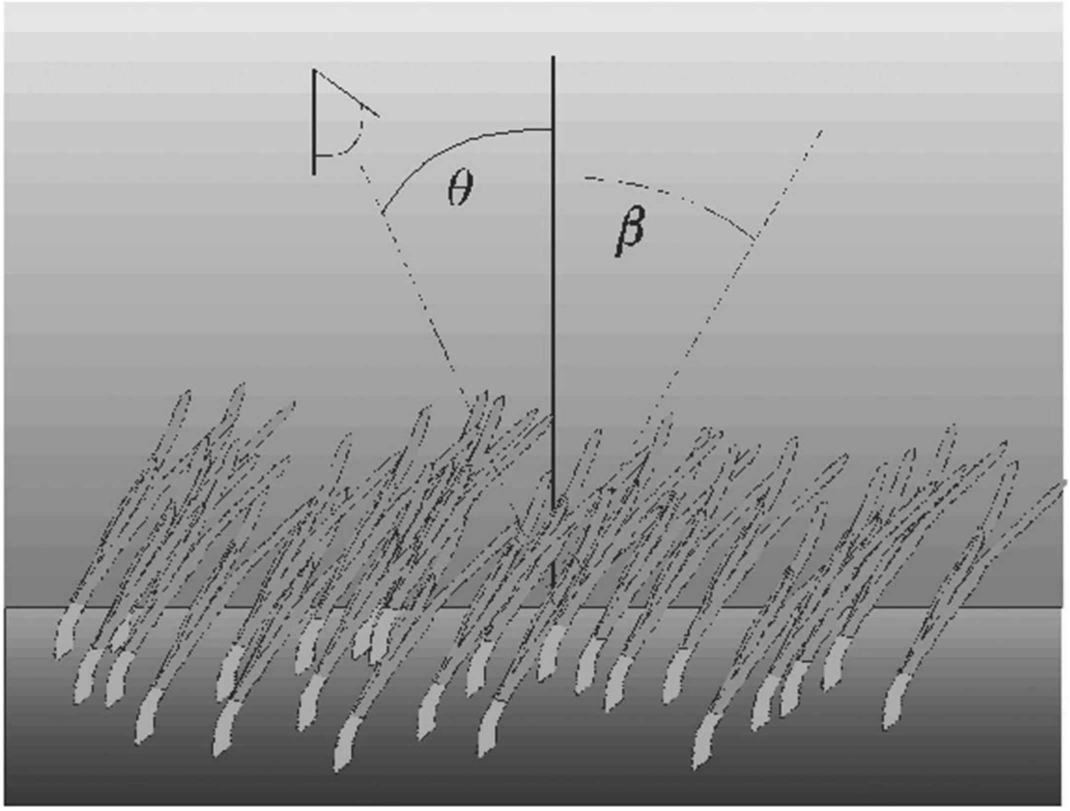

Fig. 2. Simplified angular relationships between the incident light field and the seagrass canopy. The angle of the incident light beam is indicated by the zenith angle θ. Leaf orientation is defined by the nadir bending angle β.

depends on the horizontally projected leaf area $[l_p(z)]$, which is a function of the total leaf area in that layer $[l(z)]$ and nadir bending angle (β) of the leaf (Fig. 2):

$$l_p(z) = l(z)\sin\beta \tag{8}$$

Light absorption or reflection by the horizontally projected leaf area requires further correction for the angular distribution of irradiance incident on the leaf. The Cosine Law (see Chapter 12) defines this correction as $l_p(z)/\cos\theta$, where θ represents the zenith angle of a collimated beam incident on $l_p(z)$. The angular distribution of diffuse downwelling irradiance in natural waters is much more complex, but the *average* distribution is usefully approximated by the average cosine, denoted as $\bar{\mu}$ (see Chapter 12). Thus, the ratio $l_p(z)/\bar{\mu}_d$ approximates the average geometric relationship between seagrass leaves and downwelling plane irradiance.

IV. Leaf Optical Properties

The absorption and reflection of irradiance within the plant canopy is determined by the optical properties of the leaves, in addition to their geometric orientation. Seagrass leaves, like those of all photoautotrophs, contain optically active pigments. Chlorophylls (Chls) *a* and *b* are the most abundant pigments and the only ones responsible for photosynthetic light harvesting in seagrasses. Although the pigments are principally responsible for determining the absorptance (A) and reflectance (R) of the leaf, the optical properties of intact leaves result from the complex way in which the pigments are arranged within chloroplasts and cells. This “package effect” reduces the light harvesting efficiency of the chlorophyll within the leaf and flattens the absorption spectrum of the intact leaf with respect to that of the optical properties of the freely dissolved pigments (Duysens, 1956; Larkum et al., Chapter 14).

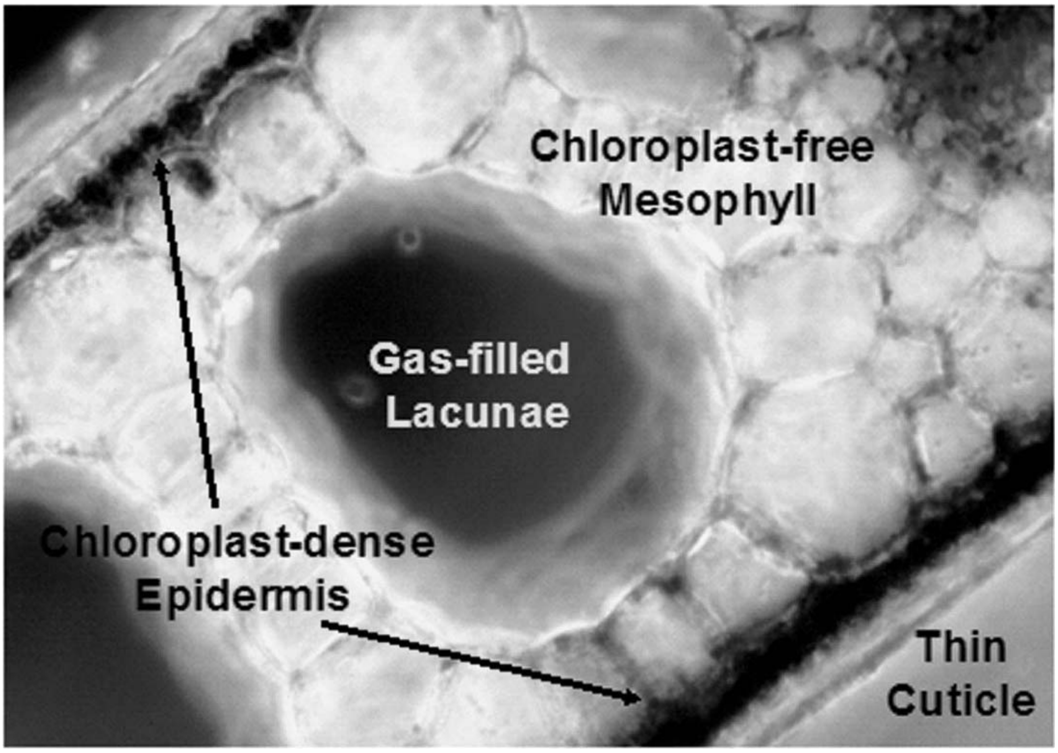

Fig. 3. Photomicrograph of a cross section of a turtlegrass leaf showing two layers of chloroplast-dense epidermis, a chloroplast-free mesophyll and air-filled lacunae running parallel to the central axis of the leaf. Image provided by F. Dobbs.

Seagrass leaf anatomy is relatively constant across species with respect to leaf thickness, chloroplast distribution, lacuna volume and even the developmental sequence leading to mesophyll differentiation (Tomlinson, 1980). Unlike terrestrial leaves, chloroplasts are restricted to the epidermis and there is no spongy mesophyll (Fig. 3). This arrangement presumably facilitates gas exchange between the leaf surface and the surrounding water. The restriction of chloroplasts to thin epidermal layers in seagrass leaves may also be advantageous in light limited environments, as has been shown for shade-adapted terrestrial leaves (Lee and Graham, 1986). This restriction, however, enhances the package effect such that large differences in leaf chlorophyll content are required to produce even minor differences between the absorption spectra of sun and shade-adapted seagrass leaves (Cummings and Zimmerman, 2003). Absorption and reflectance spectra of seagrass leaves are qualitatively typical of vascular plant and green algae pigment systems dominated by Chls *a* and *b* (Fig. 4). In general, leaves that contain higher concentrations of chlorophyll pigments have higher absorption coefficients and lower reflectances, but the differences are not linearly proportional to pigment concentration because of the package effect. For example, a 9% increase in the PAR-averaged absorptance of low light-grown eelgrass (*Zostera marina* L.) leaves relative to turtlegrass (*Thalassia testudinum* Banks ex König) leaves from a high light, tropical environment required a five-fold increase in Chl $a + b$ content (Cummings and Zimmerman, 2003). Despite the structural restrictions on chlorophyll distribution that produce strong package effects, clean seagrass leaves (even those with relatively little chlorophyll) can absorb at least 75% of the incident light, even in green biased light environments. This is similar to the absorptances of higher plant leaves and thalli of macrophytic algae (Givnish, 1987; Smith and Alberte, 1994). Scattering caused by refractive index changes at the lacuna/tissue boundaries may promote light absorption by increasing the effective optical pathlength within the leaf, but this has not been investigated in detail.

Measuring the optical properties of intact leaves requires the use of a spectrophotometer fitted with

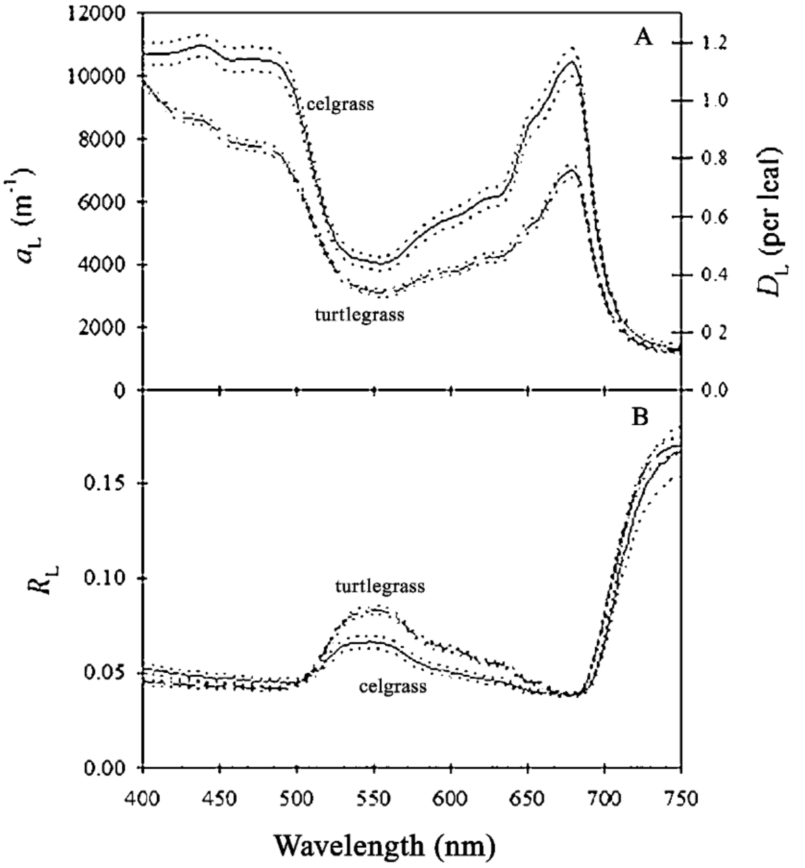

Fig. 4. Optical properties of eelgrass and turtlegrass leaves. (A) Absorption spectra plotted as absorption coefficients (left axis, per m of leaf thickness) and as optical density (right axis, per unit leaf thickness). (B) Reflectance spectra. Note that absorption is lower, and reflection is higher from the less pigmented turtlegrass leaf. From Zimmerman (2003). Copyright (2003) by the American Society of Limnology and Oceanography, Inc.

an integrating sphere that permits accurate measurement of the scattered radiant flux emanating from turbid samples (Fig. 5). The spectrophotometrically measured optical density [$D(\lambda)$], however, results from both the absorption and reflectance, or backscattering of light emanating from the leaf surface. Consequently, the raw optical density must be transformed into leaf absorptance (A_L) and corrected for leaf reflectance (R_L) in order to calculate the light absorbed by the canopy:

$$A_L(\lambda) = \left(1 - 10^{-D(\lambda)}\right) - R_L(\lambda) \quad (9)$$

The absorptance then must be transformed into an absorption coefficient [$a_L(\lambda)$], which represents the probability of photon survival, for use in the radiative transfer calculation described below:

$$a_L(\lambda) = \frac{-\ln[1 - A_L(\lambda)]}{t_L} \quad (10)$$

Although $A_L(\lambda)$ represents a dimensionless ratio [see Eq. (2)], $a_L(\lambda)$ assumes units of inverse meters (m^{-1}) by virtue of its normalization to leaf thickness (t_L).

V. Radiative Transfer and Submerged Plant Canopies

We now employ radiative transfer theory to provide a robust framework for developing a mechanistic models of the submarine light environment, system-level productivity and remotely sensed reflectance of seagrass meadows in optically shallow waters. Exact solutions to the radiance transfer equations have been developed for natural waters in which the optical medium is a continuous material composed of randomly arranged scattering elements

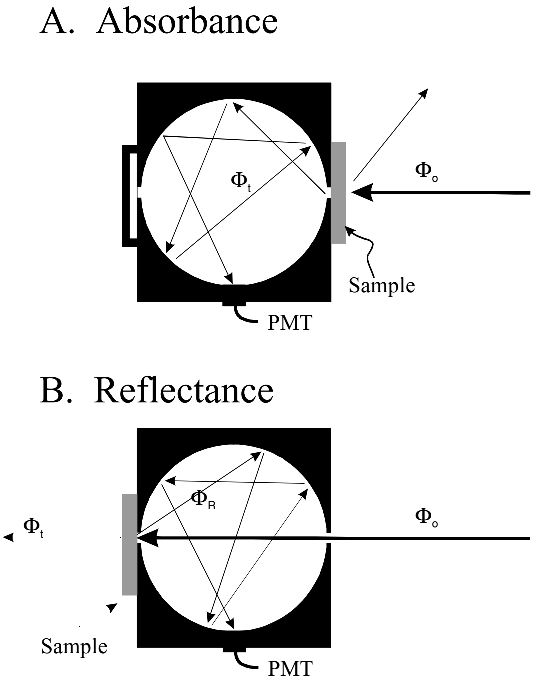

Fig. 5. Orientation of leaf samples with respect to the integrating sphere and incident light beam (Φ_0) for measurement of (A) leaf absorbance, D and (B) leaf reflectance, R. PMT refers to the photon detector, in this case a photomultiplier tube. From Drake et al. (2003). Copyright (2003) by the American Society of Limnology and Oceanography, Inc.

separated by large distances relative to the wavelength of light (Mobley, 1994). Leaves of submerged plants, however, represent discrete and densely packaged optically active material embedded in a water column of much lower optical density, which violate the homogeneity and single-scattering assumptions of the exact solutions. Dense medium radiative transfer theory is a difficult subject and it is not clear how one would obtain or measure the single scattering inherent optical properties of plant leaves to parameterize such a model for these complex structures. Consequently, models of irradiance distribution in plant canopies must rely on more empirical relationships for which light attenuation by the bulk canopy can be derived from the apparent optical properties of individual leaves (Goudriaan, 1988; Shultis and Myneni, 1988; Ganapol and Myneni, 1992). Here we employ a two-flow approach that provides a simple, quasi-mechanistic framework for understanding the relationship between water column optical properties, seagrass canopy architecture, leaf optical properties and irradiance distributions in submerged plant canopies. A more detailed discussion of this approach, and its sensitivity to various parameter values can be found in Zimmerman (2003).

We began by dividing the canopy into a series of discrete layers, of thickness Δz, into which the leaf biomass $[B(z)]$ has been partitioned vertically and projected onto a horizontal orientation [Eqs. (3)–(8)]. We now rearrange and expand the Lambert-Beer model [Eq. (1)] to approximate the downwelling plane irradiance emerging from layer (z) within the canopy:

$$E_d(\lambda, z) = E_d(\lambda, z-1)[1 - R_d(\lambda, z)] \times \exp\left[-a_L(\lambda) t_L \frac{l_p(z)}{\bar{\mu}_d(z)} - K_d(\lambda, z)\Delta z\right] \tag{11}$$

In this expanded form, $E_d(\lambda, z-1)$ represents the spectral downwelling plane irradiance incident on layer z of the canopy. The term $[1 - R_d(\lambda, z)]$ accounts for the loss of downwelling spectral irradiance by upward reflection back into layer $(z-1)$. The canopy reflectance $[R_d(\lambda, z)]$ from layer z depends on the reflectance spectrum of pure leaves $[R_L(\lambda)]$ normalized to the horizontal silhouette of leaf area and the average cosine for downwelling irradiance:

$$R_d(\lambda, z) = R_L(\lambda) \frac{l_p(z)}{\bar{\mu}_d(z)} \tag{12}$$

The amount of light transmitted through layer (z) is controlled by the exponential loss term

$$\left[-a_L(\lambda) t_L \frac{l_p(z)}{\bar{\mu}_d(z)} - K_d(\lambda, z)\Delta z\right]$$

that includes both canopy and water column effects. If there is no leaf biomass in layer (z) [i.e. if $l_p(z) = 0$], $R_d(\lambda, z) = 0$ and the exponential attenuation of light is determined by the attenuation coefficient of the water and the thickness of the water column [i.e.,$-K_d(\lambda, z)\Delta z$]. Note, however that the value of $K_d(\lambda, z)$ is both wavelength and depth dependent. Attenuation of light by the canopy, then, is defined by the product of the leaf absorption coefficient $[a_L(\lambda)]$, the thickness of the leaf (t_L), and the geometric correction factor defined as $l_p(z)/\bar{\mu}_d(z)$. The value of the average cosine

$[\bar{\mu}_d(z)]$ can be approximated by making a few simple, but relatively robust assumptions. Although we do not know enough about the scattering properties of seagrass leaves to develop more mechanistic radiative transfer models, this lack of detailed mechanistic understanding is common to most plant canopy models. Consequently, bulk scattering within the canopy is often simulated by assuming that scattering is hemispherically isotropic (bi-lambertian) about the leaf surface (Shultis and Myneni, 1988). This means that scattering by the leaf canopy will cause the average cosine for downwelling irradiance to become increasingly isotropic [i.e., $\bar{\mu}_d(z) \to 0.5$] in proportion to the horizontally projected leaf area in each layer through which the light passes. It also means that the light attenuation coefficient for the water column $[K_d(\lambda, z)]$ will increase with depth in proportion to $\bar{\mu}_d$ (Zimmerman, 2003). Mathematically, this effect can be implemented as:

$$\begin{aligned}\bar{\mu}_d(z) &= \bar{\mu}_d(z-1)\\ &\quad - \{[\bar{\mu}_d(z-1) - 0.5]l_p(z)\}\end{aligned} \tag{13}$$

where the notation $(z-1)$ refers to the value of $\bar{\mu}_d$ for light entering layer (z). Upon reaching the sea floor, a portion of the light is reflected back in the upward direction. This reflected light is then attenuated by the plant canopy and water column along its path back to the sea surface in a process symmetrical to that for downwelling irradiance:

$$\begin{aligned}E_u(\lambda, z) &= \{[E_d(\lambda, z)R_d(\lambda, z+1)]\\ &\quad + E_u(\lambda, z+1)\}\,[1 - R_u(\lambda, z)]\\ &\quad \times \exp\left[-a_L(\lambda)t_L\frac{l_p(z)}{\bar{\mu}_u} - K_u(\lambda)\Delta z\right]\end{aligned} \tag{14}$$

The total upward irradiance incident on layer $z, \{[E_d(\lambda, z)\,R_d(\lambda, z)] + E_u(\lambda, z+1)\}$, represents the sum of the downward irradiance reflected from, and the upward irradiance propagated through the layer $(z+1)$ below. In reality, the downwelling irradiance incident on layer z also includes some upwelling light reflected downward by upper layers of the canopy. This two-flow approach, however, ignores the secondary reflection, which is so low $[E_u(\lambda, z)\,R_u(\lambda, z-1) < 0.005E_d(\lambda, z)]$ that its contribution to $E_d(\lambda, z)$ is extremely difficult to measure practically, and its contribution to photosynthesis is insignificant.

VI. Irradiance Distributions Within the Seagrass Canopy

The two-flow approach described above provides a mechanistic density dependence to the determination of in-canopy light fields [Eqs. (11) and (14)], by linking absorption and reflection to leaf area $[l(z)]$ in each layer, and, therefore, the total leaf area index (L) of the canopy. Self-shading within the canopy, however, is ultimately determined by the projected leaf area $[l_p(z)]$, which is a function of leaf orientation as well as shoot density. The vertical distribution of spectral downwelling irradiance $[E_d(\lambda, z)]$ predicted by the model for a moderately dense canopy (h_c = 0.367 m, density = 458 shoots m^{-2}, L = 1.85) of turtlegrass growing at 4 m depth in the Bahamas Bank showed very good agreement with measured spectra (Fig. 6A). The irradiance spectrum at 0 m (open circles) represented the boundary condition at the top of the canopy, 3.6 m below the surface of the water. Both predicted and observed $E_d(\lambda, z)$ decreased down through the canopy. Predicted $E_d(\lambda, z)$ was within 1.2% (RMS) of the measured spectrum at the midpoint of the canopy (0.2 m into the canopy), and within 2.5% of the measured spectrum near the bottom (0.3 m into the canopy, Zimmerman, 2003).

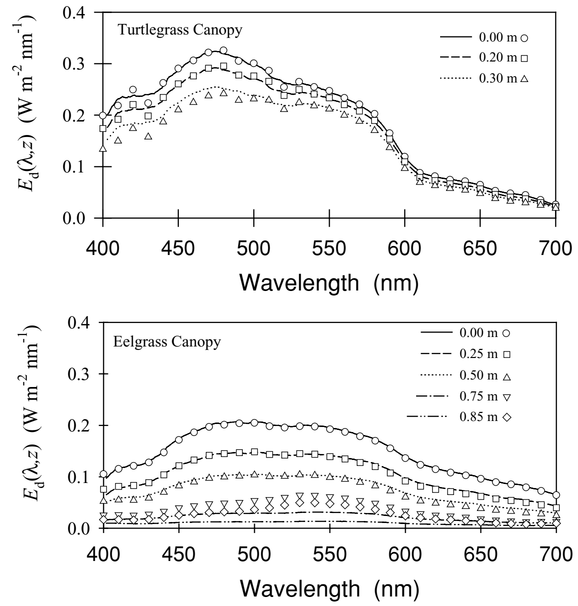

Fig. 6. Measured (lines) and modeled (symbols) downwelling irradiance spectra of the submarine light fields within a turtlegrass canopy, and an eelgrass canopy. From Zimmerman (2003). Copyright (2003) by the American Society of Limnology and Oceanography, Inc.

Simulated downwelling irradiance in a taller, denser and more heavily pigmented eelgrass canopy ($h_c = 1.0$ m, shoot density = 110 shoots m^{-2}, $L = 2.72$) submerged in the turbid waters of Elkhorn Slough, California, USA were within 15% of measured $E_d(\lambda, z)$ throughout the canopy (Fig. 6B). The RMS difference between modeled and measured spectra was 2.3% at 0.25 m, 1.5% at 0.5 m, 8.7% at 0.75 m and 14% at 0.85 m depth. The model predicted $E_d(\lambda, z)$ to peak more strongly in the green in the two bottom layers (0.75 and 0.85 m) of the canopy than was measured. Flattening of the measured spectra at the lower depths, however, may be attributed the effects of leaf epiphytes that were not accounted for in the model simulation (but see Drake et al., 2003) and to potential distortion of the measured spectra caused by low signal:noise in the red and blue portions at energy fluxes below 0.05 W m^{-2} nm^{-1}.

VII. Productivity and Carbon Balance in Submerged Plant Canopies

Equations (11) and (14) provide the total plane irradiance incident on layer (z) by quantifying the separate contributions of the canopy and the water column to the process of light attenuation. The photosynthetically used radiation [$PUR(z)$] within that layer, however, represents only the amount of light absorbed by the seagrass canopy for photosynthesis. *PUR* is less than the total irradiance attenuated by the canopy [$E_d(\lambda, z-1) - E_d(\lambda, z)$], which includes losses due to reflection and non-specific absorption. The calculation of $PUR(z)$ requires spectral integration of the total plane irradiance normalized by the photosynthetic absorptance [$A_p(\lambda)$] of the leaf and the horizontally projected leaf area [$l_p(z)$]:

$$PUR(z) = \sum_{\lambda} A_p(\lambda) l_p(z) \left[\frac{E_d(\lambda, z-1)(1-R_d)}{\bar{\mu}_d(z-1)} + \frac{E_u(\lambda, z+1)(1-R_u)}{\bar{\mu}_u(z+1)} \right] \quad (15)$$

where, the photosynthetic absorptance [$A_p(\lambda)$] represents the leaf absorptance [$A_L(\lambda)$] corrected for nonspecific absorption [$A_L(750)$]:

$$A_p(\lambda) = A_L(\lambda) - A_L\,(750) \quad (16)$$

Although the two-flow equations are equally valid whether irradiance is expressed in terms of energy or quanta, the stoichiometry of photosynthesis requires that we express $PUR(z)$ in quantum units, where:

$$\text{quanta s}^{-1} = \text{Watts} \cdot \lambda \cdot 5.03 \times 10^{15} \quad (17)$$

Knowledge of $PUR(z)$ allows the instantaneous biomass-specific photosynthesis rate of layer (z) to be calculated using the cumulative one-hit Poisson function, which provides a mechanistic relationship between photosynthetic yield and the amount of light absorbed by the leaf (Falkowski and Raven, 1997):

$$P(z) = l(z) P_{\max} \left\{ 1 - \exp\left[-\frac{\phi_p PUR(z)}{P_{\max}} \right] \right\} \quad (18)$$

In this relation, $P_{\max}$ represents the light-saturated rate of biomass-specific photosynthesis and ϕ_p is the quantum yield of photosynthesis (mol C mol^{-1} *PUR*). The quantum yield of photosynthesis is usually determined by measuring the rate of photosynthesis with monochromatic light over a range of non-saturating intensities. It also requires knowledge of A_p. It should not be confused with the more commonly reported (and more vaguely defined) α, which represents the slope of photosynthesis vs. *incident*, not absorbed, light. The use of *PUR* provides a weighted mathematical description of photosynthesis based on spectral leaf absorptance rather than unweighted absorption of broadband irradiance (i.e. PAR). Light-limited conditions, imposed either by water column turbidity or by accumulation of leaf epiphytes, bias the irradiance spectrum toward the green due to the selective absorption of blue light by photosynthetic competitors. PAR models can overestimate productivity in green light as much as twofold simply because of the spectral bias in available light vs. that absorbed by the photosynthetic pigments (Morel, 1978; Vergera et al., 1997). Consequently, the accurate assessment of photosynthetically utilized radiation becomes increasingly important in eutrophic environments that support dense populations of phytoplankton and epiphytes. Epiphytes clearly have an effect on the optical properties and production dynamics of seagrass leaves (Drake et al., 2003). Accurately modeling their effects on the irradiance distribution within seagrass canopies, however, will require better quantitative understanding of epiphyte distributions, and their optical properties, along leaf axes and across leaves of different age.

Knowledge of the instantaneous photosynthesis rate in layer (z) allows us to calculate whole canopy production (P_c) by summation of $P(z)$ over all layers (z):

$$P_c = \sum_z P(z) \tag{19}$$

Daily integrated production of the canopy can be calculated from iterative solution of the radiative transfer and photosynthesis equations if time series of top-of-canopy irradiance [$E_d(\lambda,0)$] are available. Alternatively, the daily integrated production can be approximated as follows if the daily variation in [$E_d(\lambda,0)$] is sinusoidal:

$$P_d = T \sum_z l(z) P_{\max} \times \left\{ 1 - \exp\left[-\frac{0.67 \cdot \phi_p \cdot PUR(z)}{P_{\max}} \right] \right\} \tag{20}$$

Here, T represents the length of the daily photoperiod and 0.67 is an empirically determined constant (Zimmerman et al., 1996). The use of Eq. (20) requires $PUR(z)$ to be the photosynthetically used radiation at local solar noon. The resulting photosynthesis rates can be used to determine whole plant carbon balance by normalizing P_d to the daily respiratory demand:

$$\text{Daily } P : \Re = \frac{P_d}{(\Re_{\text{Leaf}} + \Re_{\text{Root}} + \Re_{\text{Rhizome}})} \tag{21}$$

The ratio of Daily P:$\Re$ provides a convenient index of whole plant or canopy production. Carbon accumulates and growth is possible under light-replete conditions that produce Daily$P$:$\Re > 1$. Conversely, the canopy is light limited if the Daily$P$:$\Re < 1$. Growth and survival under light limitation require mobilization of stored internal reserves, reducing the total carbon density of individual shoots and the seagrass meadow. If internal reserves are insufficient to provide for growth and survival, shoots will die and the meadow will thin.

The daily respiratory carbon demand, defined by ($\Re_{\text{Leaf}} + \Re_{\text{Root}} + \Re_{\text{Rhizome}}$), accounts for metabolic consumption by both above- and below-ground tissues. Leaf respiration is presumably constant throughout the day, but below-ground tissues are subjected to prolonged anoxia each night, since the oxygen supporting below-ground metabolism is derived from leaf photosynthesis (Smith et al., 1984). The typical metabolic response to anoxia is characterized by the Pasteur effect, in which the rate of metabolic carbon consumption increases to provide the required adenylate reducing power needed to sustain living cells. The anaerobic rate of metabolic carbon consumption by roots of eelgrass, however, slows to about 65% of the aerobic rate (Smith et al., 1984, 1988; Smith, 1989). This phenomenon probably occurs in other seagrass species as well, but has not been investigated extensively. The resulting nighttime reduction in carbon demand of below-ground tissues derived from this reverse Pasteur effect can be incorporated into the daily carbon budget by assuming that the daily period of below-ground aerobiosis corresponds to the daily period of irradiance-saturated photosynthesis (Zimmerman and Alberte, 1996; Zimmerman et al., 1994, 1997). The value of ($\Re_{\text{Leaf}} + \Re_{\text{Root}} + \Re_{\text{Rhizome}}$) is also affected by the ratio of shoot:root biomass. Typical shoot:root ratios in eelgrass range from 4 to 6, but metabolic activity of subterranean tissue decreases with distance from the meristem, (Kraemer and Alberte, 1993). When all these factors are considered, below-ground metabolism of eelgrass generates a daily carbon demand equivalent to 1 to 2 hours of irradiance-saturated photosynthesis. Below-ground carbon demand will be larger in species such as turtlegrass, in which more biomass, and therefore respiratory demand, is allocated to below-ground tissue (Fourqurean and Zieman, 1991).

VIII. Leaf Orientation, Canopy Density, and Self-Shading

The two-flow approximation outlined here provides a mechanistic link between photosynthesis-irradiance responses of individual leaves and productivity of seagrass canopies in natural light environments by defining the specific geometric and optical relationships between the intact seagrass canopy and the submarine light field. When the geometric corrections defined by l_p and $\bar{\mu}$ are not applied, P vs. E response curves produce photosynthetically saturating irradiances two to four times higher than those reported by using a collimated light source oriented perpendicular to the leaf surface,

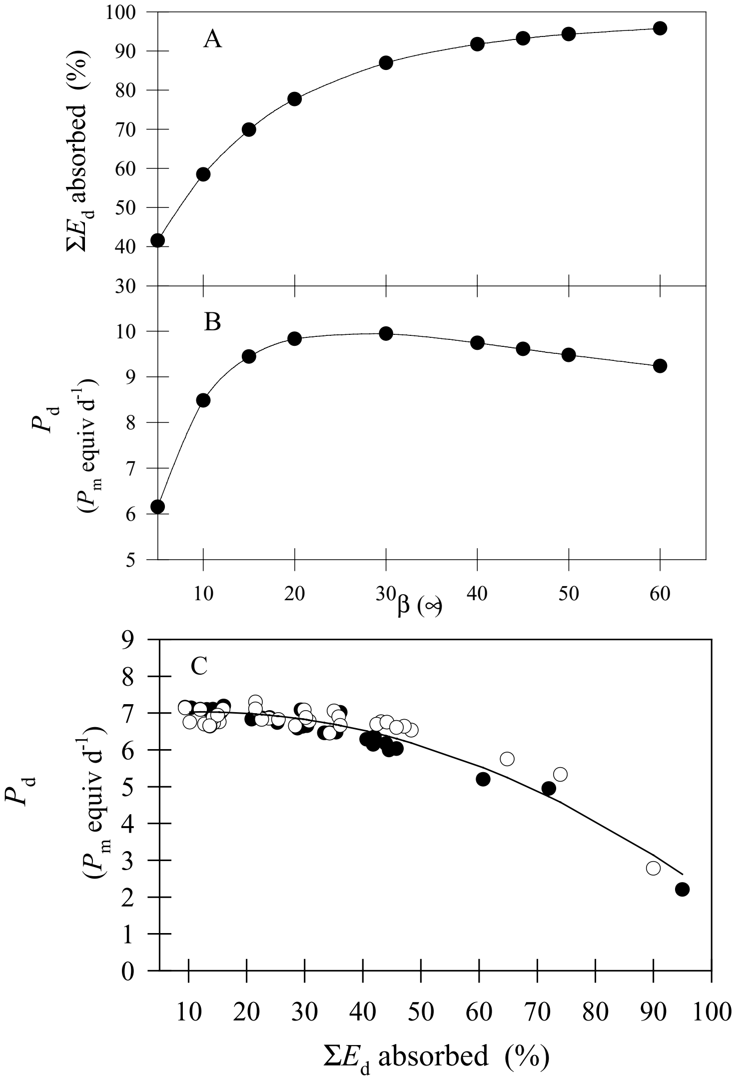

Fig. 7. Effect of leaf orientation (bending angle, β) on (A) the total light absorbed by an eelgrass canopy, and (B) the resulting shoot-specific productivity of the canopy. (C) Resulting general relationship between total light absorbed by the canopy and shoot-specific productivity for a variety of different canopies. From Zimmerman (2003). Copyright (2003) by the American Society of Limnology and Oceanography, Inc.

which can lead to large differences in production estimates (Fourqurean and Zieman, 1991; Herzka and Dunton, 1997). To illustrate the effect of leaf orientation on biomass-specific productivity of shoots within a seagrass canopy, the two-flow equations were solved for a 1-m tall eelgrass canopy growing in Elkhorn Slough as described above. The total amount of light absorbed by the canopy asymptotically approaches 100% of the incident flux as the nadir bending angle (β) of the leaves increases (e.g. from tidal current flow, Fig. 7A). Productivity of the canopy, however, is maximized at leaf bending angles between 10° and 20° (Fig. 7B). Although a more horizontal leaf orientation increases the efficiency of photon capture, most of the light is absorbed by the topmost layers of the canopy, which are already light-replete with respect to photosynthesis. Consequently, the lower portions of the canopy (where most of the biomass resides) become even more light limited, and the productivity of the whole canopy declines (Fig. 7C). This illustrates that the relationship between top-of-canopy irradiance and whole canopy productivity is necessarily a dynamic result of the physiological P vs. E response of individual

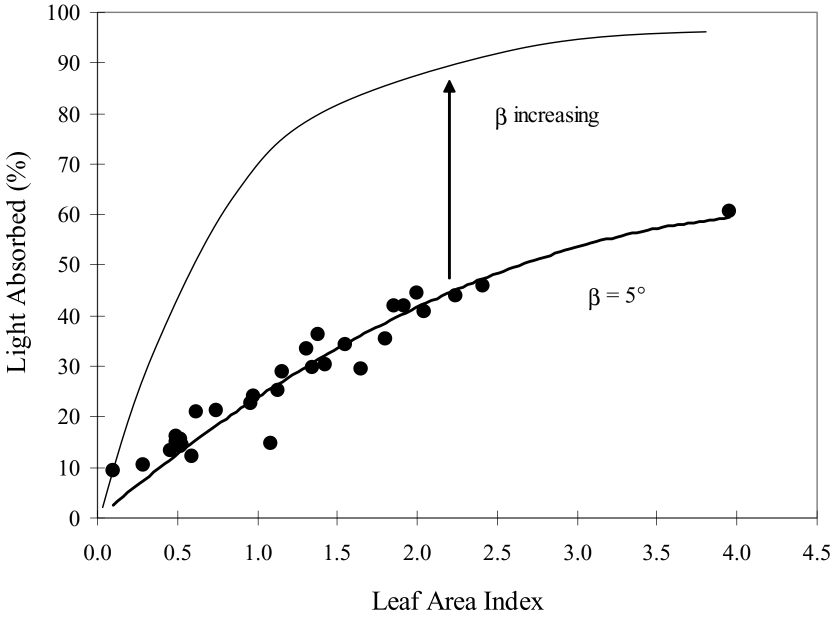

Fig. 8. The amount of light absorbed by the canopy increases non-linearly as a function of leaf area index. Symbols represent model calculations for a range of seagrass canopy architectures in which leaves were oriented 5° from the vertical (see Zimmerman (2003) for details). Increasing the leaf bending angle causes the canopy to be more effective at absorbing light, but the non-linear nature of the photosynthesis-irradiance response curve, combines with self-shading to decrease the productivity of the canopy as light absorption increases.

leaves placed within the geometric context of a moving canopy.

The two-flow equations also provide a mechanistic density dependence to the absorption of *PUR*. This density dependence is illustrated by the nonlinear increase in the total amount of light absorbed by the canopy as a function of density (Fig. 8). Bending angle further enhances the density-dependent light absorption, as shown in Fig. 7. This density dependence decreases the daily integral of shoot-specific photosynthesis (Fig. 7C), but does not materially affect whole-plant carbon demand. Consequently, the model can be used to estimate the shoot density at which photosynthesis and metabolic carbon demand of whole shoots are in balance, i.e., when $P{:}\Re = 1$. Self-shading has been incorporated into other models through a simple attenuation coefficient derived by correlation from canopy height and shoot density (Short, 1980), and as an explicit negative feedback on photosynthesis but without a direct link to the submarine light environment (Burd and Dunton, 2001). Although local correlative approaches are useful when sufficient data exist for accurate least-squares parameterization of the transfer coefficients, they are not easily generalized to other populations or environments without extensive recalibration against new data.

IX. Effects of Water Quality on Seagrass Productivity and Distribution

The worldwide decline in seagrass distribution and abundance has focused much research on the development of predictive relationships between water quality and the status of submerged vegetation (e.g. Batiuk et al., 1992; Morris and Tomasko, 1993; Berry et al., 2003). It has been argued that the sensitivity of seagrasses to light availability makes them good indicators of changes in environmental water quality (Dennison et al., 1993; Duarte et al., Chapter 11, section VI.C). Unfortunately, seagrass losses are very difficult to reverse once they are allowed to occur.

The radiative transfer approach outlined here incorporates water quality effects on the irradiance throughout the water column, as well as density-dependent effects on irradiance distribution and light utilization within the canopy. Thus, it can be used to explore water quality issues relevant to light availability that controls seagrass production and distribution *before* significant impacts occur on seagrass populations. This approach was tested as part of a pilot study designed to develop a plan for monitoring submerged vegetation resources throughout Puget Sound, Washington, USA (Berry et al., 2003). The model was used to explore the maximum sustainable eelgrass density at Dumas Bay located in the highly turbid southern region of Puget Sound. Estimates of the submarine light environment in the water column were obtained from calculations performed by the radiative transfer model *Hydrolight* (Ver 4.2 Sequoia Scientific, Inc.) for local solar noon on the spring equinox. Modeled water column Chl concentrations ranged from 20 to 50 mg m^{-3}. Total suspended solids (TSS) concentrations ranged from 0 to 25 mg L^{-1}. Model calculations of daily carbon balance produced well-behaved second-order relationships between maximum sustainable eelgrass density and depth. These simple relationships were then used to populate distribution maps of potential eelgrass density for different water quality conditions. The resulting distributions were qualitatively consistent with a field survey conducted at the site in 1995 by Norman et al. (1995) (Fig. 9). Water column turbidity was identified as a major factor determining eelgrass distributions in Dumas Bay, and model predictions were more sensitive to variations in TSS than Chl. This finding is similar to the situation in other eastern Pacific estuaries such as San Francisco Bay, where light availability is more affected by sediment load than Chl (Alpine and Cloern, 1988; Zimmerman et al., 1991, 1995). The reliability of any numerical model is always limited by the data used to parameterize the important driving variables. In this case, however, uncertainty in shoot morphology, and shoot:root ratios in particular, represented a second-order problem with regard to accurately modeling the eelgrass distribution.

X. Potential Impacts of Climate Change on Seagrass Productivity

The dramatic response to CO_2 enrichment exhibited by a number of seagrass species indicates that carbon limitation of photosynthesis may be a common feature of these submerged angiosperms (Beer and Waisel, 1979; Millhouse and Strother, 1986; Durako, 1993; Abal et al., 1994; Invers et al., 2001). Although the absolute kinetics of photosynthesis vs. $[CO_2]$ appear to be species specific (Invers et al., 2001), the response generally involves a non-linear increase in photosynthesis in response to increasing $[CO_2]$, which yields a negative response to pH (a proxy for $[CO_2]$ in seawater, Fig. 10). This effect can be easily incorporated into the biophysical model by defining P_m as a function of $\text{pH}\{= f(-\log[CO_2])\}$. In the case of eelgrass, the increase in $P_{\max}$ can be described by:

$$P_{\max} = 82\exp(-0.53 \cdot \text{pH}) \qquad (22)$$

This relation sensitizes canopy productivity and daily carbon balance calculated by Eqs. (18) to (21) to CO_2 availability. Using a similar approach to that described above for the analysis of water quality on eelgrass distributions in Dumas Bay, the potential impact of increased atmospheric $[CO_2]$ on eelgrass distribution was explored in Elkhorn Slough, California, USA, a moderately turbid estuary where eelgrass distributions are limited to less than 2 m depth (Zimmerman et al., 1994; Zimmerman and Caffrey, 2002). Patchy meadows currently occupy about 17 ha of shallow habitat along margins of the main channel of the Slough, and these realized distributions are consistent with model predictions of light-limited distribution based on average water quality conditions and bathymetry (Fig. 11). Assuming present day bathymetry and water quality, a doubled atmospheric CO_2 concentration would increase the areal coverage of eelgrass in Elkhorn Slough to 23 ha, a 35% increase over the present distribution. In addition to increasing the density of existing beds, the model predicts eelgrass to colonize the basin at the top of Seal Bend, which is presently too deep for successful vegetation. Although atmospheric CO_2 concentrations are not expected to rise to a level that prevent carbon limitation of seagrass photosynthesis, increasing the CO_2 concentration to the point where seagrass photosynthetic performance is equivalent to that of marine algae (pH 6.2) may yield a six-fold increase in eelgrass coverage and greatly increase the density of existing vegetation.

XI. Effects of Epiphytes on Leaf Photosynthesis

Seagrass leaves are colonized by a diverse array of epiphytes (Borowitzka et al., Chapter 19) that make significant contributions to the overall productivity of seagrass ecosystems (Penhale, 1977; Mazzella

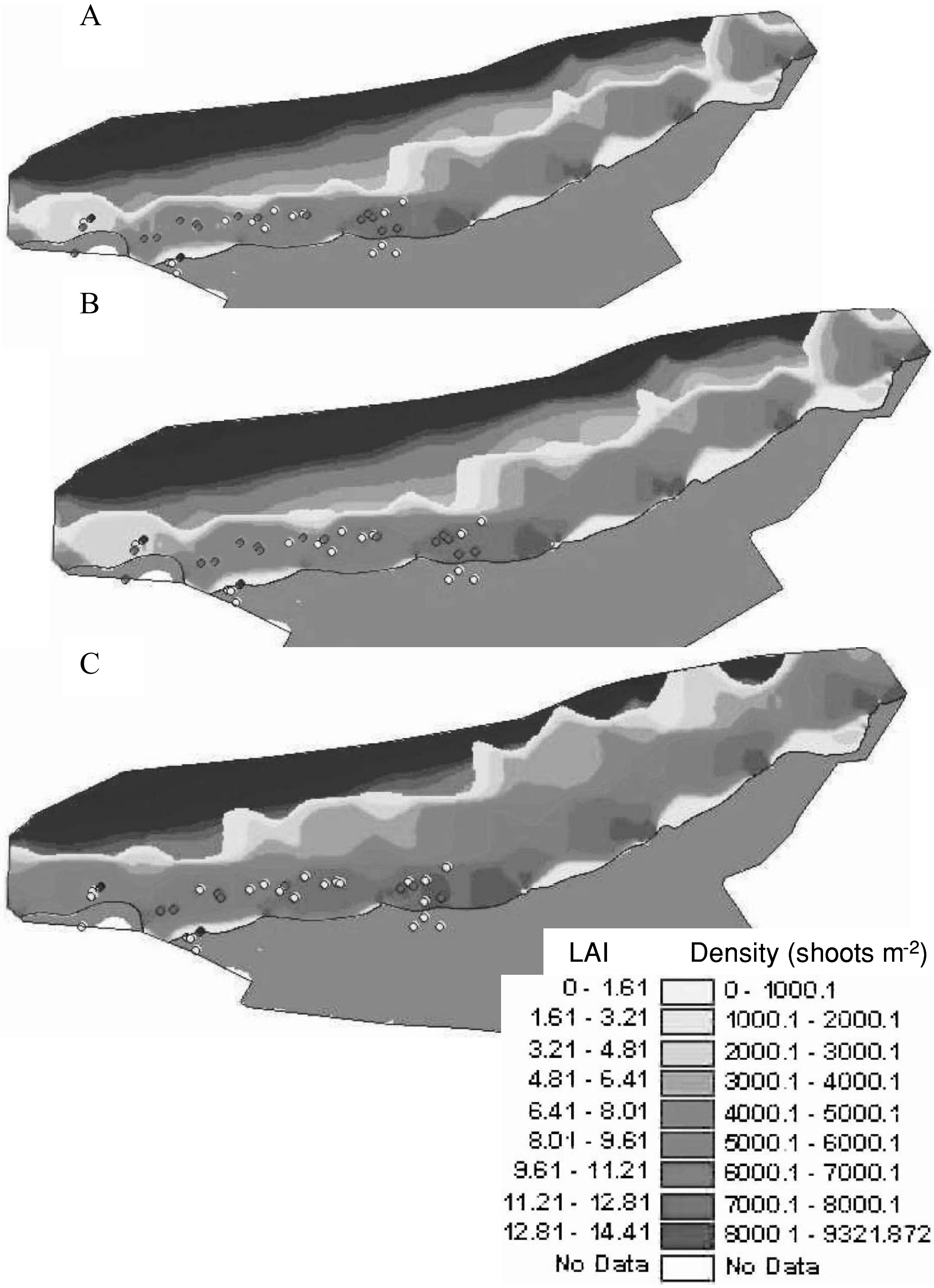

Fig. 9. Predicted eelgrass densities and depth distribution of eelgrass shoots in Dumas Bay, Washington, USA for different scenarios of water clarity. (A) 50 mg m^{-3} chlorophyll *a*, 25 mg L^{-1} total suspended solids. (B) 30 mg m^{-3} chlorophyll *a*, 25 mg L^{-1} total suspended solids. (C) 30 mg m^{-3} chlorophyll *a*, 10 mg L^{-1} total suspended solids. From Berry et al. (2003). Bathymetry is indicated by blue shading. Unvegetated tidal flats are illustrated in brown.

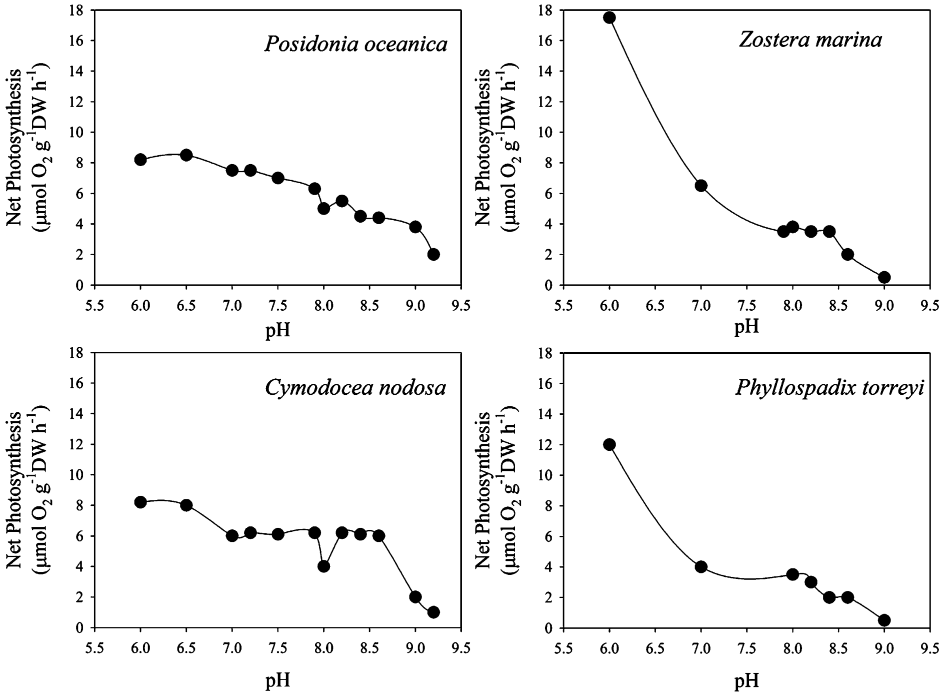

Fig. 10. Relationship between seagrass photosynthesis and seawater pH derived from manipulation of dissolved aqueous CO_2 concentrations. Redrawn from Invers et al. (2001).

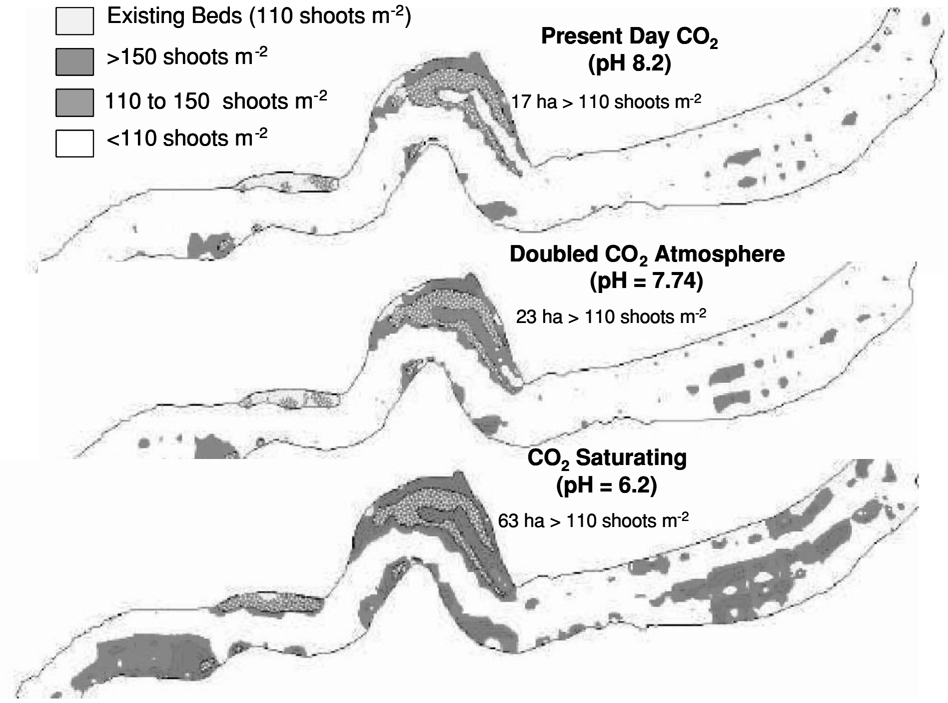

Fig. 11. Predicted effect of increased ambient CO_2 concentrations on eelgrass distributions in Elkhorn Slough, California, USA. Seal Bend is the ∩-shaped region in the middle of the channel. Elkhorn Slough drains westward into Monterey Bay (left side) from an upland watershed to the east (right side). From Zimmerman and Palacios (2002).

and Alberte, 1986; Klumpp et al., 1992). The complex biofilms produced by the growth of these organisms creates physical barriers to light absorption, gas exchange (particularly CO_2) and nutrient uptake (e.g. Sand-Jensen, 1977; Bulthuis and Woelkerling, 1983; Van Montrfrans et al., 1984), and epiphyte accumulation has been implicated as an important agent contributing to the decline of seagrass meadows in eutrophic waters (Hemminga and Duarte, 2000). It is now possible to measure the optical properties of intact leaf-epiphyte communities accurately and quantify their specific effects on leaf photosynthesis (Drake et al., 2003). Epiphytes exhibit varying degrees of chlorophyll-like absorption spectra, preferentially absorbing blue and red light. The resulting spectral bias imposed on the light actually reaching the seagrass leaf produced a two-fold greater reduction in leaf photosynthesis calculated from *PUR* relative to similar calculations based on PAR. Important challenges, however, remain with regard to the incorporation of leaf epiphytes into the vertically resolved model described here. In particular, epiphytes distributions are characterized by strong spatial gradients within and among leaves that also show significant temporal variability (Bulthuis and Woelkerling, 1983; Kirchman et al., 1984; Törnblom and Søndergaard, 1999). These relationships, their seasonal variations and responses to environmental change (eutrophication, CO_2 increase, etc.) deserve more extensive quantification.

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Chapter 14

Photosynthesis and Metabolism in Seagrasses at the Cellular Level

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I. Introduction

Seagrasses are marine angiosperms from the Families Potamagetonaceae and Hydrocharitaceae (Chapter 1). These are by origin land plants that developed both aerial photosynthesis and aerial flowering and then returned to a successful fully submerged marine habitat, from where their algal forbears derived. Following the evolution of land plants there have been few developments in terms of photosynthesis: the only outstanding developments being adaptations to arid conditions, such as the development of C_4 photosynthesis in semi-arid plants and Crassulacean Acid Metabolism (CAM) in plants from desert regions (Bowes et al. 2002). These adaptations affect morphological changes (Kranz anatomy) in C_4 plants, as well as adaptation of the initial carboxylation pathways (C_4 and CAM plants) – with, in the case of CAM plants, a temporal shift in daily uptake of CO_2(Keeley, 1982). In both cases the Benson-Calvin Cycle is retained together with a conventional set of photoreactions (photosystem I, photosystem II and Chlorophyll a/b light-harvesting complexes), as the primary mechanism of photosynthesis.

While seagrasses are unique in having returned to the sea, there are many plants that have evolved into freshwater hydrophytes (Sculthorpe, 1967; Bowes et al., 2002). Since they both live in an aqueous environment, there are close parallels in many respects between seagrasses and freshwater hydrophytes, such as the presence of a diffusive boundary layer around the leaves, a photosynthetic epidermis, loss of stomata and development of aerenchyma. Hydrophytes are found in both Potamagetonaceae and Vallisneriaceae and therefore there are also close phylogenetic relationships to consider. Much work has been carried out on freshwater hydrophytes (see e.g. Bowes et al. 2002; Maberly and Madsen, 2002) and this review will take this work into account.

A recent review of photosynthesis in seagrasses is that of Touchette & Burkholder (2000).

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II. Photosynthetic Adaptations to Marine Submergence

The clear photosynthetic adaptation to marine submergence, also seen in hydrophytes (Sculthorpe, 1967), is the conversion of the leaf epidermis to the primary site of photosynthesis, accompanied by the loss of stomata and extreme reduction of the cuticle (Larkum et al., 1989). This is presumably an adaptation to gaseous movement in a liquid medium rather than a gaseous medium, where the rates of diffusion in the latter are reduced by a factor of ca 10,000 (Larkum et al., 1989; Borum et al., Chapter 10). This primary adaptation has been accompanied by three very important adaptations also found in a number of other submerged plants and some, but not all, algae:

(i) development of biochemical mechanisms for enhanced inorganic carbon uptake, similar to the carbon concentrating mechanisms (CCMs) of some algae,

(ii) limitation of photosynthesis to the outer cell layers of the leaf or lamina and reduction in the non-photosynthetic tissues of the leaf or lamina

(iii) development of aerenchyma.

There may also be other adaptations which are poorly documented at present such as reduction in photorespiration and the Mehler ascorbate peroxidase (MAP) pathway (see Section VII) in order to counteract the high levels of oxygen generated internally in the leaf as a result of the photosynthetic epidermis and high diffusive boundary layers at the leaf surface (see e.g. Maberly and Madsen, 2002). However, both mechanisms (photorespiration and MAP pathway) play an important role in protecting seagrass leaves from damage from excess light, under exactly these conditions, so a balance has to occur. However, in freshwater hydrophytes the tendency is to thinner leaves with often just two cell layers in leaves, both photosynthetic. This is not an option in most seagrasses (*Halophila* spp. are an exception) because of wave action, which necessitates a strong, tough photosynthetic lamina.

These aspects are discussed in greater detail in the following sections

III. The Diffusive Boundary Layer (DBL)

Substantial diffusive boundary layers are found at most respiratory or photosynthetic surfaces of submerged plants, animals or bacteria (Jørgensen, 2001). The size and stability of these layers have not been explored fully in seagrasses (but see Larkum et al., 1989); however, their existence has been shown in the freshwater aquatic, *Potomageton* spp (Sand-Jensen and Revsbech, 1987) and it is certain that they exist in seagrasses. As a consequence of the DBL and the anatomy of seagrass leaves, water motion will be a critical factor in determining the rate of photosynthesis in seagrasses (Larkum et al., 1989 and this fact has been established experimentally in

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Abbreviations
α – initial rate of photosynthesis for a P vs E curve
AF – Absorptance (absorption factor).
AZ – acetozolamide
C_4 – primary photosynthetic CO_2 fixation involving production of C_4 acids
CA – carbonic anhydrase
CAM – crassulacean acid metabolism;
CCM – carbon concentrating mechanism;
C_i – inorganic carbon sources for photosynthesis;
$\delta^{13}C$ – fractionation of ^{13}C against ^{12}C compared to belemnite standard
D1 – major polypeptide of PSII which binds Q_A and partly P_{680}
E_c– irradiance at the compensation point (older symbol, I_c)
ΔF – fractional yield of maximum fluorescence in actinic light
DBL – diffusive boundary layer
F_m – maximum fluorescence yield
$F_m{}'$ – maximum fluorescence yield in actinic light
F_o – minimum (dark) fluorescence yield
F_t – fluorescence yield at time T in actinic light
F_v – variable fluorescence yield
E – photon flux density
E_K – E at which slope of light limiting region of the light curve (α) intercepts Pmax (older term, I_k)
ETR – electron transport rate
GC-MS – gas chromatography-mass spectrometry
MAP – Mehler ascorbate peroxidase (pathway)
NADP – nicotinamide dinucleotide phosphate
NPQ – non-photochemical quenching
NSCC – non-structural carbohydrate carbon
P_{max} – maximum rate of photosynthesis
PAM – pulse amplitude modulated (fluorometry)
PAR – photosynthetically active radiation
PQ – photochemical quenching
PSI – photosystem I
PSII – photosystem II
qE – energy dependent quenching of fluorescence yield
qN – quotient of non-photochemical quenching
qP – quotient of photochemical quenching
Q_A – plastoquinone acceptor of PSII
Q_B – secondary plastoquinone acceptor of PSII
RLC – rapid light curve
Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase
UV-B – ultraviolet B radiation

a few studies (Fonseca and Kenworthy, 1987; Koch, 1994, Koch and Gust, 1999; see also Koch et al., Chapter 8). However, no studies to date have effectively shown how the hydrodynamic properties of various seagrass leaves are related to photosynthetic rates under different degrees and types of water motion. Presumably it is an important factor in the depth and spatial distribution of many seagrasses, as it is in freshwater hydrophytes (Maberly and Madsen, 2002) and in algae and many other plants (Raven, 1970, 1997). Hydrodynamic properties must also be an important factor in the regulation of seagrass primary production, particularly in tropical seagrasses exposed to supersaturating irradiances for more than half of the solar day.

IV. Inorganic Carbon Uptake Mechanisms

Seagrasses generally live in full seawater (33‰) at a pH of ca 8.2 and a bicarbonate (HCO_3^-) concentration of ca 2 mol m^{-3} (Larkum et al., 1989). Under these conditions there is very little CO_2 available (ca 10 mmol m^{-3}, at 25°C). Thus while CO_2 is the substrate for Rubisco, the primary enzyme for C_i fixation in photosynthesis, the most available source of inorganic carbon (C_i) is HCO_3^-. Therefore it is not surprising that many seagrasses have mechanisms for the uptake of HCO_3^- or its conversion to CO_2 near the leaf surface; whether all seagrasses have these mechanisms is not fully documented but it seems likely. It has been claimed that seagrasses do not have the efficiency of marine algae to concentrate C_i (Björk et al., 1997), but this needs further justification. However, on theoretical grounds it can be shown that many seagrasses must be limited by the supply of C_i under P_{max} conditions (Larkum et al., 1989).

A theoretical scheme for the uptake of CO_2 and HCO_3^- was presented by Larkum et al. (1989) which involved (i) active acidification of the cell wall and DBL (to increase the concentration of CO_2), (ii) the secretion of the enzyme carbonic anhydrase (CA), which catalyzes the interconversion of CO_2 and HCO_3^-, into the same space, and (iii) at least one active HCO_3^- uptake system (and probably more – see below).

Since that time the basic details of this proposal have been supported by a number of studies and the current situation is summarised in Fig. 1 (based substantially on that given in Larkum et al. 1989).

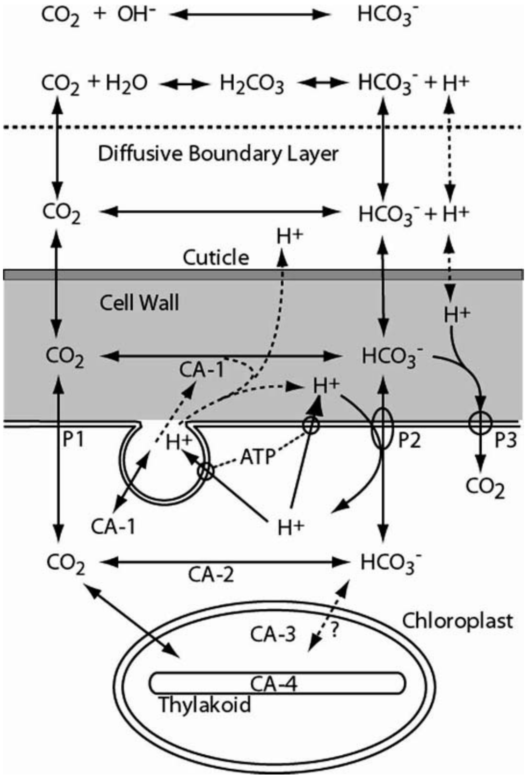

Fig. 1. Schematic diagram indicating the possible pathways for entry of CO_2 and HCO_3^- to the photosynthetic epidermis of seagrass leaves. P1, P2 and P3 refer to three different "pumps" by which C_i can be actively transported into the epidermal cells across the plasmalemma (see Text for details).

The role of active uptake, i.e. energy-dependent uptake, of CO_2 and HCO_3^- has been explored in a number of seagrass studies, as described below. However, this area of study has advanced much more in Cyanobacteria and eukaryotic algae where the simpler and more manipulable (genetic) systems allow conclusions to be drawn with greater certainty, although even here the final story is yet to be told. In these systems it has been concluded that there are at least two active HCO_3^- uptake systems and possibly also an active CO_2 pump, as well as passive diffusion of CO_2 (Badger et al., 2002). An external CA is important but so is the presence of various CAs in the chloroplast and in the carboxysome in Cyanobacteria or the pyrenoid, if present, in eukaryotic algae. A carbon concentrating mechanism has been found to be present in both Cyanobacteria and many eukaryotic algae (Badger et al., 2002; Raven and Beardall, 2003), which is dependent on these various pumps, and CAs. It can be seen therefore that the situation in seagrasses is likely to be complex and provide a rich source of studies for several years to come. The present evidence is summarised in the next paragraph.

The early work of Millhouse and Strother (1986a,b, 1987) suggested that there is a salt-stimulated HCO_3^- pump in *Z. muelleri* as well as CO_2 uptake. A HCO_3^- pump has been supported by a number of more recent investigations (Beer and Rehnberg, 1997, Beer et al. 2002, Invers et al. 1999a,b, 2001). Beer and Rehnberg (1997) compared photosynthetic rates at pH 8.2 and 9.0. It was deduced that HCO_3^- was acquired by an extracellular CA-induced dehydration to CO_2, prior to C_i uptake. The HCO_3^- transport appeared to be ATPase-mediated. Invers et al. (2001) obtained quantitative information on the relative role of CO_2 and HCO_3^- uptake mechanisms by analysing the rate of C_i uptake at a range of $[CO_2]$ and $[HCO_3^-]$. This gave clear evidence of a HCO_3^- mechanism but showed that *P. oceanica* and *Cymodocea nodosa* had higher capacity for HCO_3^- uptake than *Z. marina* or *Phyllospadix torreyi*. A significant recent advance came with the finding that external buffers can inhibit the uptake of C_i in *Z. marina*, *Halophila stipulacea* and *Ruppia maritima* (Hellblom et al., 2001, Beer et al., 2002). Beer et al. (2002) present further evidence, in addition to buffering capacity, to suggest three mechanisms of carbon acquisition, (i) a CA-dependent CO_2 mechanism (P1, Fig. 1), (ii) a proton/HCO_3^- symport mechanism (P2, Fig. 1) and (iii) a CA-linked HCO_3^- mechanism carrying CO_2 into the cytoplasm (P3, Fig 1). Clearly there is the possibility for all these mechanism, and more, based on what we know from Cyanobacteria (Badger et al., 2002). A feature mentioned above, and shown in Fig. 1 is the ATP-linked pumping of protons into the cell wall, and potentially the DBL. This active mechanism is involved in two C_i pumping mechanisms, at least (mechanisms (i) and (ii) above). The role of Na^+ suggested by Millhouse and Strother (1986 a,b, 1987) could be linked to the pumping of C_i (either by a Na^+ ATPase or by a sodium-stimulated system (see Ritchie et al., 1996) or to an antiport exchange diffusion process such as a Na^+/H^+ system.

Evidence for acidification of the cell wall and DBL comes from studies of the buffer Tris in *Z. marina*, *H. stipulacea* and *R. maritima* (Hellblom et al., 2001; Beer et al., 2002), where it was concluded that proton extrusion, and the maintenance of acidic zones in the diffusion boundary layer, is of importance for supplying C_i to the photosynthesising cells. However, this result is possibly compromised because of the known inhibitory effect of Tris on photosynthesis, admittedly in isolated chloroplasts (Yamashita and Butler, 1968). The presence of an external carbonic anhydrase has been indicated by an inhibitory effect of acetozolamide (AZ) on photosynthesis (James and Larkum, 1996; Invers et al., 1999a,b, Schwarz et al., 2000, Hellblom et al., 2001). However, this result is also now compromised since it is known that several C_i pumps incorporate a CA, which is therefore potentially inhibited by an external (non-membrane-penetrating) CA inhibitor such as AZ (see below).

Despite these advances there is still much left to do in seagrasses, in documenting DBLs, and C_i uptake mechanisms. The relict cuticle and its effect on resistance to C_i movement is an area where no research has been carried out. Also $\delta^{13}C$ ratios in seagrasses are not fully documented (Raven et al., 2002). However, those values that do exist (*Amphibolis spp, Phyllospadix scouleri, Thalassia testudinum, Z. marina, Z. nova-hollandiae*) indicate values in the range -8 to -14. These values are less negative than those often quoted and much less negative than in extreme examples (eg. certain red algae with values more negative than -30 -Raven et al., 2002). These levels indicate that seagrasses overcome any diffusive limitation of C_i uptake due to a DBL and a relict cuticle by deploying an active C_i uptake mechanism, probably by an HCO_3^- uptake mechanism (Raven et al., 2002).

V. Rates of C_i Uptake

A large number of studies have focussed on P vs E (P vs I) curves for photosynthesis in seagrasses over the last 20 years. The results are summarised in Table 1. Unfortunately standardisation of results is clearly lacking, which makes direct comparisons difficult in many cases. The major factor as discussed above is that rates are strongly dependent on stirring: only at the highest stirring rates will the DBL be thin and allow for maximum photosynthesis. Therefore a number of reported values of P_{max} will have been done under stirring-limited conditions and this accounts for some variability in results. Nevertheless the high photosynthetic rates support previous views on the high productivity of seagrasses notwithstanding the

Table 1. Photosynthetic and respiratory characteristics of seagrass leaves: α, rate of photosynthesis in the linear part of the P vs E curve; E_k, PAR at the intersection of the α: curve with P_{max} in a P vs E curve: P_{max}, maximum rate of photosynthesis (without photoinhibition or without other stresses such as restricted C_i supply); Ec, PAR at the compensation point — the point at which gross photosynthetic rate equals the respiratory rate; PAR, photosynthetic radiation (μmol photons m^{-2} s^{-1}); R, respiratory rate. Units as follows: α: 1. μg O_2 ug^{-1} chl h^{-1}; 1A μM O_2 mg Chl^{-1} min^{-1}; 1B. nmol O_2 mg Chl^{-1} m^2; 2. mg O_2gDW^{-1} h^{-1}; 2A. μgO_2 $gAFD^{-1}$ min^{-1}; 3. μm O_2 gFW^{-1} min^{-1}; 4. μmol O_2 m^{-2} s^{-1}; 4A μmol O_2 cm^{-2} $h^{-1}(\mu E\ m^{-2}\ s^{-1})$; 5. mg O_2 gDW $h^{-1}(\mu mol\ E\ m^{-2}\ s^{-1})^{-1}$; 6. μm O_2gDW-1 h-1(μE. m^{-2} $s^{-1})^{-1}$; 7. mg C gDW-1 h-1; P_{max} and Leaf Respiration, R: 8. mg O_2 g^{-1} h^{-1}; 8A μg O_2 $gAFDW^{-1}$ min^{-1}; 9 μg O_2 μg Chl^{-1} h^{-1}; 9A. μmol O_2 mg Chl^{-1} min^{-1}; 10. μmol O_2 gDW^{-1} h^{-1}; 11. ppm O2 gDW-1 h-1; 12. μmol CO_2 $kgDW^{-1}$ s^{-1}; 13. μmol O_2 m^{-2} s^{-1}; 14. μmol O_2 gFW^{-1} min^{-1}; 15. mgC gDW^{-1} h^{-1}; 16. μmol O_2 cm^{-2} h^{-1}.*

Species	α	E_k*	P_{max}	E_c*	R	Conditions	Reference
Amphibolis antarctica	0.039–0.054 (1)	32–40	1–1.5 (8)	17–23	0.3–0.6 (8)	13–23°C	Masini & Manning 1997
Amphibolis griffithii	0.035 (1)	70	2.4 (9)	20	0.51 (8)	Gross Pmax	Masini et al. 1995
Amphibolis grififthii	0.039 (1)	25–56	1–1.35 (8)	15–17	0.3–0.5 (8)	13–23°C	Masini & Manning 1997
Cymodocea nodosa	0.046 (2)		8.4 (8)	61	2.4 (8)	20°C	Enríquez et al., 1995
Cymodocea nodosa	0.005–0.63 (2)	2.4–8	2.4–8.0 (8)		0.29–0.64 (8)	10 or 30°C	Terrados & Ros 1995
Halodule uninervis	–	50	0.12 (8A)	20–40			Beer & Waisel, 1982
Halodule wrightii	0.5–2.4 (2)		374 (10)	85	75–116 (10)	In situ	Dunton & Tomasko, 1994
Halodule wrightii	0.5–2.4 (2)	319	422 (10)	81	37–142 (10)	In situ, yearly mean	Dunton, 1996
Halophila stipulacea	–	100	40 (9A)	20–40		Variable depth	Beer & Waisel
Posidonia australis	0.009 (1)	90	0.84 (9A)	25	0.3–0.9 (1)	Gross Pmax	Masini et al. 1995
Posidonia australis	0.015–0.024 (1)	35–50	0.8–2.0 (8)	17–20	0.3–0.6 (1)	13–23°C	Masini & Manning 1997
Posidonia oceanica	0.046 (5)		6.99 (8)	21	0.97 (8)	20°C	Enriquez et al., 1995
Posidonia oceanica	0.01 (2)	257	7.7 (8)	37	1.0–1.4 (8)	Yearly mean	Alcoverro et al. 1998
Posidonia sinuosa	0.016–0.019 (1)	55–59	0.8–1.1 (9)	24	0.39–0.94 (9)	Gross Pmax	Masini et al. 1995
Posidonia sinuosa	0.015 (1)	38–55	0.6–1.2 (8)	20–25	0.36–0.57 (8)	13–23°C	Masini & Manning 1997
Ruppia maritima	0.062 (2)	–	15.9 (8)	23	1.43 (8)	20°C	Enríquez et al., 1995
Syringodium filiforme	0.5–0.6 (6)	320–410	200–216 (10)	125–140	29–37 (10)	Seasonal	Major and Dunton, 2000
Thalassia testudinum	0.017 (5)	–	2.1–2.3 (16)	–	0.16–0.18 (16)	Shallow, dense community	Enríquez et al., 2002
Thalassodendron ciliatum	30–50	1.5–5	30–50 (12)	–	–	0.5–33 m depth	Parnik et al. 1992
Zostera capricorni	0.018 (4)	182	4.2 (13)	45	–	–	Flanigan & Critchley, 1996
Zostera marina	0.0035 (3)	100–290	0.5–1.7	–	–	Seasonal	Zimmerman et al. 1995
Zostera marina	0.002–0.004 (1A)	65	0.4 (9A)	10–15	–	15–35°C	Marsh et al., 1986
Zostera marina	0.008 (7)	250	3–6.5 (15)	30–35	–	Young leaf segments	Jiménez et al. 1987
Zostera marina	0.046 (5)	–	6.85 (8)	40	1.7 (8)	20°C	Enriquez et al., 1995
Zostera marina	0.00133 (1B)	27	0.2 (9A)	–	0.07 (9A)	15°C	Zimmerman et al., 1997
Zostera noltii	0.23–0.63 (2A)	222–390	71–236 (8A)	98–300	–	Seasonal	Vermatt & Verhagen 1996
Zostera noltii	0.008 (7)	350	3–6.5 (15)	30–35	–	Young leaf segments	Jiménez et al., 1987
Zostera noltii	0.046 (5)	–	12.1 (8)	56	2.7 (8)	20°C	Enríquez et al., 1995

high respiratory load imposed by a leaf anatomy with the major photosynthetic layer limited to the epidermis and a large underground (non-photosynthetic) component. In terms of maximum photosynthetic rate, seagrass leaves are not the highest of photosynthetic tissues/communities (Krause-Jensen and Sand-Jensen, 1998) but they are in the mid to upper range. It should also be remembered that such rates often focus on rates under optimum conditions.

A number of other studies have focussed on such important topics as photosynthetic performance with depth (e.g. Olesen et al., 2002) and variations along a single leaf (e.g. Enriquez et al., 2002), as well as many studies on such environmental factors as temperature and salinity.

VI. Photosynthetic Efficiency, Light-Harvesting and the Package Effect

Seagrasses like all aquatic plants are shade-adapted (Reiskind et al., 1989; Bowes et al., 2002), i.e. they show light saturation at fairly low irradiances and have a high α (initial slope of the P vs E curve). Like all angiosperms they have the ability to vary their photosynthetic apparatus to optimise use of the available light but have only a small ability to do this in the short-term (that is in minutes to hours) by state transitions (whereby light capture by the two photosystems is manipulated—see section VIII.I). As shade plants they optimise to rather high levels of light harvesting proteins per photosystem (high absorption cross-section) and can also vary the number of photosystems per unit of thylakoid membrane and the number of chloroplasts per cell (Major and Dunton, 2000, 2002: Cummings and Zimmerman, 2003). However, unlike many land plants with complex photosynthetic anatomies (eg palisade and spongy mesophyll) which allows them to harvest light more efficiently (Lee et al. 1990), seagrasses rely almost entirely on a photosynthetic epidermis, limiting their ability to efficiently harvest available light (Cummings and Zimmerman, 2003).

Light harvesting in seagrasses has been studied by Major and Dunton (2000, 2002), in *Thalassia testudinum* and by Cummings and Zimmerman (2003) in *T. testudinum* and *Z. marina*. All these studies show that photoacclimation is largely brought about by changes in the chlorophyll content per unit surface area (or unit weight). Chlorophyll content was shown to vary up to five fold (Cummings and Zimmerman, 2003). Major and Dunton (2002) showed that the unit size (absorption cross-section) of photosystem I increased under low light but found that neither photosystem density (per unit chlorophyll) or the unit size (absorption cross-section) of photosystem II changed, again consistent with a shade strategy. One way for increased photosynthesis is to increase the absorptance of a leaf by increasing the number of chloroplasts or by rearranging chloroplasts in or out of the light path (Schwarz et al., 2002). As the number of chloroplasts in the light path increases the absorption of light approaches a black body absorber (Larkum and Barrett, 1991). The result is that chloroplasts deep in the tissue (or on the under side of leaves which undergo little displacement) receive a very-much modified spectral radiation, rich in green light. This is a consequence of the package effect, the tendency for densely packed chlorophyll to absorb greater amounts of violet and red light, compared to green light. A photosynthetic system without suitable pigments such as phycobiliproteins to harvest green light can nevertheless harvest most of the available light, but only at the expense of an inefficient use of the available photosynthetic apparatus, in this case deeper chloroplasts which work at low efficiency. The package effect has been directly demonstrated in two seagrasses, *T. testudinum* and *Z. marina* (Cummings and Zimmerman (2003; see also Zimmerman, Chapter 13).

Parts of the leaves, usually the younger parts, deeper down in the canopy are also subject to this effect since the package effect means that red and blue light are differentially absorbed, dependent on shoot density and current velocity, in the upper canopy region (Zimmerman, 2003; Zimmerman, Chapter 13). Since seagrasses show reasonable photosynthetic efficiencies, on the basis of incident photons, compared with other plants (Major and Dunton, 2002, Cummings and Zimmerman, 2003) they clearly provide the necessary photosynthetic machinery for optimum light absorption despite the metabolic costs of providing that machinery.

The total primary productivity of seagrasses varies from quite high to moderate, in comparison with the most highly productive land plants and algae (Larkum, 1981; Duarte and Chiscano, 1999). This has generally been seen as caused by deployment of a large underground rhizome and root system, rather than leaves inefficient in photosynthesis. (Raven, 1984). However, as shown by Duarte and Chicano (1999) the biomass ratios and production ratios of above-ground to below-ground parts varies widely in seagrasses, so that future work should focus on just how much the proportion of below-ground parts influences overall primary production and changes with depth (see eg. Olesen et al., 2002). Some seagrasses such as *Posidonia oceanica* and *P. australis* tend to have a very high proportion of underground parts while other seagrasses such as *H. ovalis* tend to have a low proportion, which may be analogous to the division between woody and herbaceous terrestrial plants. This overriding factor must strongly influences primary production rates, but other factors such as nutrient supply and latitude (Duarte and Chicano, 1999) have so far hindered a clear assessment of what ultimately controls primary production in seagrasses compared to, for example, algae, such as *Ulva lactuca,* which have a photosynthetic lamina in which the majority of cells are photosynthetic, and with almost no other parts (Longstaff et al., 2002). Current technology now provides the means to answer many of these outstanding questions. However, it should be kept clear that in such studies there are two scales involved, that of photosynthesis and primary production over hours to a single day, usually under optimal conditions, and that over a year, subject to herbivory, storm damage and a variety of other environmental conditions.

VII. Mechanisms of CO_2 Fixation, CAM, Photorespiration and Oxygen Cycles

It appears that seagrasses inherit a typical Calvin-Benson Cycle. The first fixation products (<10 s) are often typical of a Calvin-Benson Cycle (Benedict et al., 1980 for *Thalassia testudinum*; Larkum, unpublished for *P. australis*). However, in two other seagrasses (*Zostera noltii*, Beer et al., 1980, and *Halophila beccarii*, Waghmode and Joshi, 1983) evidence has been obtained for early production of C_4 acids. This latter evidence need not necessarily point to true C_4 metabolism and evidence of a much more concerted kind (detailed metabolic schemes and appropriate enzymes, such as PEP carboxylase, pyruvate-phosphate dikinase, NADP malate dehydrogenase, and various decarboxylases such as NADP-specific malic enzyme) would be needed to indicate that a true C_4 metabolism exists. There is rather more evidence that a concerted β-carboxylation mechanism exists in some freshwater hydrophytes (Bowes et al., 2002), suggestive of C_4 metabolism. However, of over 7600 C_4 species only about 10 aquatic species have been identified and in several of these the photosynthetic tissue in question is aerial. The submerged aquatics *Hydrilla verticillata* and *Egeria densa* have been identified as C_4 NADP-specific malic enzyme species (Bowes et al., 2002). However, even in those freshwater hydrophytes, which show the most evidence for C_4 metabolism, there is no evidence of Kranz anatomy, which is so typical of terrestrial C_4 plants. Thus there may be a possibility for this kind of metabolism in seagrasses, which also show no sign of Kranz anatomy (Kuo and den Hartog, Chapter 3).

In the past, C_4 metabolism has been assumed on the basis of $\delta^{13}C$ evidence: C3 plants have high values of -20 to -30 whereas C_4 plants have values of -10 to -15. On this basis early assessments indicated that seagrasses were C_4 plants. However, this was before it was realised that large diffusive boundary layers would also generate low negative values of $\delta^{13}C$. Based on this, many early workers questioned the evidence (see references in Abel and Drew, 1989). More recent analyses have also excluded the possibility of C_4 metabolism in seagrasses on the evidence from $\delta^{13}C$ experiments (Durako, 1993; Raven, 1997; Raven et al., 2002).

Crassulacean acid metabolism (CAM) is another means by which terrestrial plants have adapted the basic Calvin-Benson Cycle by interpolating β-carboxylation metabolism: in this case by temporally shifting the C_i uptake period to night-time. Several cases of CAM-type metabolism have been found in marsh plants or freshwater aquatics, the most studied of which is the genus *Isoetes* (Keeley, 1982). In terrestrial CAM plants CO_2 is taken up at night to reduce water loss. In freshwater hydrophytes the strategy appears to be to take up C_i when it is most freely available, i.e. at night, rather than during the day when it is restricted and only accessible through a large DBL. Such a strategy could benefit seagrasses. Just one report exists on the presence of a CAM-like behaviour of non-photosynthetic cells of leaves of *Thalassodendron ciliatum* (Parnik et al., 2002). However, until more evidence is provided it is safer to assume that no C_4- or CAM-type photosynthesis occurs in seagrasses.

Evidence on the existence of photorespiration in seagrasses (Fig. 2) is poor, but what evidence there is seems to suggest that it is rather lower in seagrasses than in terrestrial plants (Abel and Drew, 1989; Frost-Christensen and Sand-Jensen, 1992).

Classically, in this process, phosphoglycolate is produced by the competitive reaction of O_2 with RuDP catalysed by Rubisco (Lorimer, 1981). From there glycolate is formed in the chloroplast, by dephosphorylation, and is transported to peroxisomes where it is oxidised by glycolate oxidase (consuming molecular oxygen), and transaminated to form glycine. Then with the help of mitochondria the glycine is decarboxylated (with the formation of carbon dioxide) and the carbon skeleton recycled through the peroxisome and the chloroplast, finally, being converted to glycerate and glycerate-1-phosphate, which can re-enter the Calvin-Benson Cycle. A key product is therefore the presence of glycolate. Glycolate is certainly found in seagrasses using ^{14}C techniques (Larkum, unpublished). The presence of peroxisome-like bodies has also been documented (Kuo, 1989). However, direct quantitative data on the activity of photorespiration in seagrasses is lacking. In theory, if this process is very active it could consume a large amount of the oxygen produced in photosynthesis. This would constitute a futile cycle with no competitive advantage, yet it might be an unavoidable process due to the high O_2 levels in epidermal cells caused by the leaf anatomy and the surrounding DBL (see Section III). On the other hand some of the excess O_2 might be consumed under these circumstances by the operation of a Mehler Ascorbate Peroxidase (MAP) pathway (Fig. 2; Miyake & Asada, 2003). In this process a Mehler reaction intercepts the electrons coming out of the reducing side of PSI (which would normally be delivered to $NADP^+$) as follows

$$2O_2 + 2e^- \rightarrow 2O_2^- \text{ (non-catalyzed reaction at reduced ferredoxin)}$$

$$2O_2^- + 2H^+ \rightarrow O_2 + H_2O_2 \text{ (catalyzed by Fe superoxide dismutase)}$$

The hydrogen peroxide produced is then detoxified with ascorbate peroxidase:

$$2H_2O_2 + \text{ascorbate (oxidised)} \rightarrow 2H_2O + \text{ascorbate (reduced)} + O_2$$

The reduced ascorbate is re-oxidised by a glutathione/NADPH system. Overall, 1 O_2 is reduced and 2 H_2O are produced by PS I while in photosynthesis 2 H_2O are consumed and 1 O_2 are produced by PS II, i.e. there is no net O_2 exchange. Thus there is no net build up of oxygen. *If such a pathway were to be up-regulated during periods of high electron transport rate (ETR), i.e. under high PAR, then excess concentrations of O_2 could be avoided.* Whether such a process actually takes place is not known. There is evidence for such processes in algae (Miyake & Asada, 2003), but an investigation of the role of competing processes in *Ulva lactuca* (Longstaff et al., 2002), under high light, concluded that this pathway could account for only a small fraction of the flow of electrons and that cycling around PSII was a more substantive process in discharging excess energy from absorbed photons. A diagram to illustrate the competing pathways for photosynthetically generated electrons and energy is given in Fig. 2.

From this section it can be seen that there is much still to be done on the photosynthetic metabolism of seagrasses before we know the various processes in detail. Work on freshwater aquatics has advanced much further in the last decade than in seagrasses (see, eg., Bowes et al., 2002; Maberly and Madsen, 2002).

VIII. Fluorescence Studies

Chlorophyll *a* fluorescence techniques provide a very powerful tool to understand a wide range of photokinetic processes associated with photosynthesis in seagrasses. Several types of fluorometer are available; these include the Pulse Amplitude Modulated (PAM; Schreiber et al., 1986; Schreiber, in press), non-modulated PEA (Plant Efficiency Analyser; Strasser et al., 2000) system and the Fast Repetition Rate (FRR) fluorometer (Gorbunov et al., 2000). To date, the majority of seagrass fluorescence research has been performed with the Diving-PAM and current research is examining such topics as extremes of light adaptation and acclimation (specifically addressing the questions: how can seagrasses tolerate extended periods of low light and how can intertidal seagrasses survive photodamage from excess irradiance) and effects of pollution. Seagrasses generally function as shade-adapted plants. However, tropical seagrasses can be exposed on a daily basis to photoinhibitory levels of light (i.e. in excess of requirements), while for some temperate seagrasses, usually growing in light-limited environments, there may be severe stress when they are exposed intertidally on cloudless days in summer. The use of fluorescence techniques to monitor anthropogenic stress is dealt with in Ralph et al., Chapter 24.

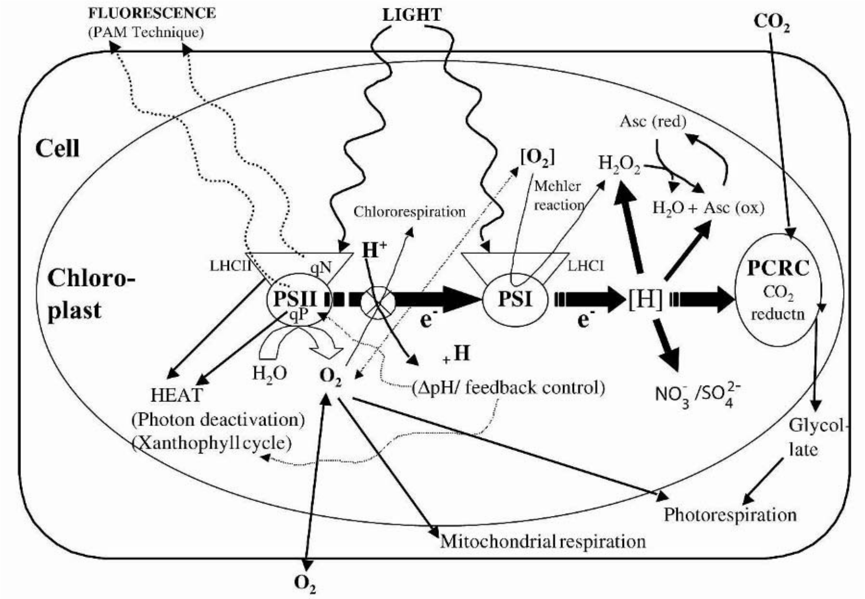

Fig. 2. A diagram to illustrate the competing pathways for photosynthetically generated electrons and energy. In the light, electrons flow from water through PSII and PSI to ferredoxin and $NADP^+$ (represented here by [H]), driven by the reactions centres of PSII and PSI. Fluorescence comes mainly from PSII and is highest when electron flow from PSII to PSI is restricted. This occurs immediately after turning on the the light after a prolonged period of darkness, when the activity of the photosynthetic carbon reduction cycle (PCRC) (Calvin- Benson Cycle) is low. It can also occur after a supersaturating flash of light or when the supply of C_i is restricted. Under these conditions $NADP^+$ and ATP build up and restrict electron transport from PSII. Also the buildup of ATP causes the lumen of thylakoids to acidify (low pH), which in turn activates on heat dissipation via the xanthophyll cycle. When PCRC activity is low, or light intensity is high, electron transport can be channelled to H_2O_2 (MAP pathway) and nitrate and sulfate reduction. LHCI and LHCII are the Chl $a + b$ antenna systems of PSI and PSII, respectively. When the flow of electrons through PSII is higher than through PSI, Q_A and Q_B become reduced and fluorescence approaches a maximum, and electron flow a minimum (photochemical quenching, qP, is high); at the same time acidification (low pH) leads to heat dissipation via the xanthophyll cycle (qN is high)) and via the reaction centre of PSII itself. See text for details.

A. A Chlorophyll Fluorescence Fundamentals

Pulse Amplitude Modulated (PAM) fluorescence can be used to study such components of photosynthesis as photosynthetic capacity, photosynthetic efficiency and electron transport rate. When a leaf is exposed to a saturating flash (0.8 s, 2000–3000 μmol photons m^{-2} s^{-1}) the fluorescence yield initially increases rapidly to a peak and then slowly declines (quenches). This fluctuation in the fluorescence signal is known as the “Kautsky” curve (see Fig. 3). Measuring various cardinal points along this curve allows insight into the dynamic changes in photosynthesis or photokinetics. **Variable fluorescence** is the difference between maximum fluorescence yield (F_m) (when all reaction centres are closed) and initial fluorescence (F_o) (when all reaction centres are open). Initial, dark fluorescence (F_o) is generally fairly stable, for a healthy plant at a given time, but can increase with photodamage (loss of active reactions centres). F_m, the maximum fluorescence, is much more sensitive to conditions: it can decrease under a number of stress conditions (photoinhibition, salt stress, water stress, high and low temperature, presence of toxicants, etc.) and also under elevated light, as more energy is dissipated as heat (i.e. non-photochemical quenching). F_m can be measured by first adapting the sample to darkness for a reasonable period (ca. 20 min) and then exposing to actinic light of moderate levels (= 5–100% sunlight irradiance) or to a supersaturating flash of light.

Maximum quantum yield of PSII (**F_v/F_m** = $[F_m - F_o]/F_m$) is a measure of the PSII photochemical efficiency, which is useful for understanding the physiological state of PSII, as well as the effect of environmental stresses mentioned above (Schreiber and Bilger 1993; Maxwell and Johnson 2000). Theoretically, F_v/F_m should not be affected by non-photochemical quenching (NPQ), since the tissue is assumed to be dark-adapted. However, after

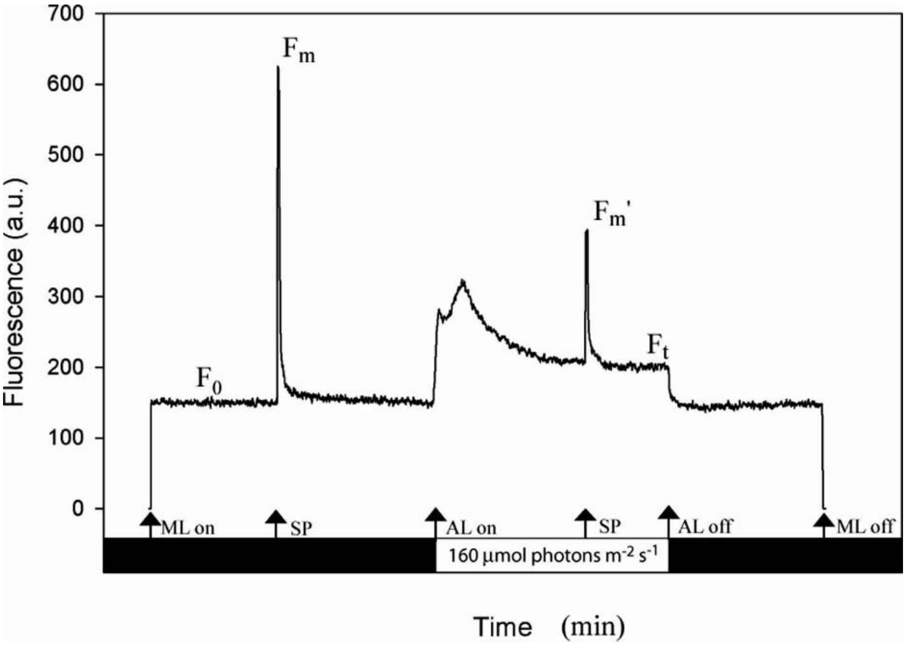

Fig. 3. A typical fluorescence curve for a seagrass leaf measured with a pulse amplitude modulated (PAM) fluoroimeter (Walz Co., Effeltrich, Germany) showing light and dark-adapted measurement of quantum yield. ML is measuring light, SP is saturating pulse and AL is actinic light. (Unpublished data of P.J. Ralph).

dark-adaptation (20–30 min) there may still be some xanthophyll cycle activity and this would reduce F_v/F_m. A decrease in the F_v/F_m ratio can be a result of either an increase F_o or a decrease F_m (Major and Dunton 2002).

Effective quantum yield ($\Delta F/F'_m$ = ($F_m' - F_t)/F'_m$) is a measure of PSII quantum yield in the light. The steady state level of maximum fluorescence in the light (F'_m) is measured by giving a short saturating pulse of light after a period of constant actinic light with steady level of fluorescence yield (F_t). Effective quantum yield (Φ_{PSII}) is therefore more complex than maximum quantum yield (F_v/F_m), as it is influenced by the stoichiometry of PSII: PSI, by Calvin-Benson cycle activation, by photo-inactivation of PSII centres and by the xanthophyll cycle activity (Demmig-Adams and Adams, 1993). Effective quantum yield requires the photosystems to be operational, which usually means that it is under some degree of light pressure.

The two primary mechanisms for relaxing the fluorescence yield are photochemical (qP) and non-photochemical quenching (qN or NPQ) (Fig. 2). Photochemical quenching (qP) and effective quantum yield ($\Delta F/F'_m$) both measure the photochemistry of PSII. However, $\Delta F/F'_m$ measures both active and inactive PSII reaction centres, while qP only measures the efficiency of active PSII RCs. Both qN and NPQ describe non-photochemical quenching. However, NPQ is the preferred measure, as it does not require knowledge of minimum fluorescence (F_o) and measures photoprotective mechanisms that are used to dissipate excess energy. A rapid decrease in Fm’ is usually linked to the build-up of a proton gradient across the thylakoid membrane, while the proton gradient is lowered by ATP synthase, which produces ATP to be consumed in the Calvin cycle. NPQ can be separated into 3 components based on the speed of relaxation; these are energy-dependent quenching (qE), state transition quenching (qT) and photoinhibitory quenching (qI) (Horton and Hague 1988). The dynamics of the NPQ components are presently unknown for seagrasses, and once this is understood we will be better able understand how they utilize the available irradiance and maintain photosynthesis under variable light climates. qE is generally directly related to the activity of the xanthophyll cycle in higher plants (Demmig-Adams and Adams, 1993). The maximum quantum yield is always greater than effective quantum yield, usually as a result of non-photochemical quenching lowering the $\Delta F/F_m'$.

Photosynthetic processes linked to inorganic carbon fixation are dealt with in Section IV of this chapter; however, several issues related to fluorescence are discussed here. The redox state of the primary electron acceptor (Q_A) and the fluorescence emission is influenced by CO_2 fixation processes. Therefore, $\Delta F/F_m'$, qP and qN are influenced by Rubisco activity, which has a feedback loop to the electron transport rate (Fig. 2). Therefore, fluorescence can potentially be used to assess inorganic carbon (C_i) uptake (Schwarz et al. 2000; Hellblom et al., 2001; Beer et al., 2002), where it was shown that the photosynthesis of *H. ovalis* and *C. serrulata* were limited by inorganic carbon availability.

B. Photosynthetic Rates: Electron Transport Rates (ETRs)

Conventionally photosynthetic rates have been measured by the rates of evolution of O_2 or the uptake of CO_2. However, the electron transport rate (ETR) through PSII is directly related to both the former rates and can therefore be used to measure rates of photosynthesis (Genty et al., 1989). ETR can be calculated from the effective quantum efficiency ($\Delta F/F_m'$), the absolute amount of incident irradiance (PAR), the absorption of that irradiance and the partitioning of incident irradiance between the two photosystems, a follows:

$$\mathrm{ETR} = \Delta F/F_m{}' \times \mathrm{PAR} \times 0.84 \times 0.5.$$

Several assumptions are implicit in the use of ETR; firstly 0.5 defines the probability of a photon being captured by either PSII or PSI; secondly, the determination that the percent absorption of photons is approximately 84% (0.84) is based on terrestrial leaves (Genty et al., 1989). However, percent absorption (absorption factor) has been found to vary from 44–72% for seagrasses (Durako and Kunzelman 2002). So, to eliminate those assumptions, it has been recommended to use relative ETR (rETR), which is simply determined by $\Delta F/F_m{}' \times$ PAR (Beer and Björk 2000, Beer et al., 2000). This simple and practical approach assumes constant absorptance along and between leaves; however, Enriquez et al. (1992) were able to show absorptance varied along leaves, between leaves and between species (88.5% for *P. oceanica* and a minimum of 49.8% for *H. wrightii*). The Imaging PAM (Walz, Effeltrich) allows accurate determination of absorption factors and this instrument can therefore be used to determine absorption factors of seagrass leaves, although not in situ (see section VIII.J).

C. Rapid Light Curves

In photosynthetic studies, photosynthetic rate versus light (P vs E) curves are very common (see Table 1 for seagrass studies). In these studies, the photosynthetic rate is usually measured after a relatively long time in any given light regime (10 min to several hours). Rapid light curves (RLCs), are measured over a period of only minutes (i.e. 10–30 s per light regime), since PAM fluorometers allow for very quick measurements of ETRs. RLCs provide a snapshot of the light adaptation state of the photosynthetic tissue and tell us about the immediate physiological state of the tissue. However, they do not necessarily give curves similar to classical P vs E curves and their use has to be carefully considered.

Basically, using RLCs, the fluorometer determines the effective quantum yield at the end of a series of short (10 s) actinic light exposures. As light increases, the effective quantum yield decreases as NPQ increases. Since qE, the major component of NPQ (see above) is related the activity of the xanthophyll cycle (Demmig-Adams and Adams, 1993) the RLC will depend on the light history (Hader et al., 1998) and genetic type of the tissue studied. Shade plants tend to entrain the xanthophyll cycle less actively than sun plants. In turn, sun plants take a period of up to several hours to entrain the xanthophyll cycle. Thus, the degree to which an RLC will reflect xanthophyll cycle activity (and NPQ) will depend on the type of tissue used, its previous light history and the (dark) relaxation time of the xanthophyll cycle in the given tissue. Care also has to be taken to avoid effects of state transitions, which fortunately are fairly small in higher plants (Larkum, 2003).

D. Diurnal Fluctuations of Photosynthesis

As with all higher plants, seagrasses have diurnal patterns of photosynthetic activity, which vary according to the daily cycles of irradiance, as well as the daily tidal cycle. Seagrasses have the ability to tolerate high light during solar noon by dynamically down-regulating their photosynthetic apparatus (Ralph et al., 1998). This process, whereby excess irradiance is dissipated as heat without being absorbed into the photosystems and without causing damage, is largely entrained by the xanthophyll cycle (see below). In the absence of down-regulation, seagrasses can suffer photoinhibition by excess irradiance. Photoinhibition is the caused largely by irreparable damage to D1 protein of PSII necessitating the replacement of the damaged D1 protein. An essential aspect of understanding the dynamic nature of diurnal rhythms is the ability of PSII to recover during the afternoon or overnight, i.e. a recovery from photoinhibition over a period of hours in the shade or overnight.

Seagrasses growing near the intertidal region will be exposed to high light stress, which can result in either down-regulation or, if irradiance is sufficiently high, can result in photoinhibition. Photoinhibition can be defined as damage to the PSII reaction centres, mainly to D1 protein, requiring several hours of low light (or overnight) for repair. Down-regulation is associated with increased NPQ. Photoinhibition is generally associated with reduced F_v/F_m and with increase in F_o.

E. Xanthophyll Cycle

The xanthophyll cycle is well understood in terrestrial plants (see eg. Demmig-Adams and Adams (1993). However, recent evidence indicates that the xanthophyll cycle is an integral component of the seagrasses as well (Ralph et al., 2002). In the xanthophyll cycle, increased energy dissipation (NPQ) is linked to an increase of the pH gradient across the thylakoid membrane, which in turn triggers the xanthophyll cycle (Fig. 2). The xanthophyll cycle is dependent on three xanthophylls: light triggers the conversion of the low-light form of violaxanthin to the epoxidised (high-light) form, zeaxanthin, and the intermediate, antheraxanthin. *Zostera marina* shows distinct changes in xanthophyll pigments composition that is linked to diurnal light fluctuations and these changes are also correlated to a down-regulation of photochemical efficiency, a decline in $F_m{}'$ and an increase in NPQ (Ralph et al. 2002). Once the minimum saturating irradiance was exceeded, all violaxanthin was converted to antheraxanthin and zeaxanthin. Unusually high levels of antheraxanthin were found in *Z. marina* suggesting incomplete conversion to zeaxanthin.

F. Photoinhibition and UVB Inhibition

As described above photoinhibition, is defined as damage to PSII, principally due to damage to D1 protein (section VIII.D). This is in contrast to down-regulation, which is reversible in a matter of hours and is sometimes referred to as dynamic photoinhibition. If the rate of D1 repair is less than the rate of damage, then photoinhibition is said to have occurred (Flanigan and Critchley 1996). Photoinhibition occurs most severely with shade-adapted plants, such as seagrasses, and recovery requires a relatively long time (6 h to several days, depending strongly on ambient temperature). Photoinhibition is characterized by a sustained decline in effective quantum yield. High light can cause substantial damage to PSII of seagrasses (Ralph and Burchett 1995) and a large component of this is due to damage to D1 protein (Flanigan and Critchley 1996). Flanigan and Critchley (1996) found the maximum rate of D1 synthesis occurred at 350 μmol photons m^{-2} s^{-1} in *Z. capricorni*, whilst photoinhibition occurred at about 1100 μmol photons m^{-2} s^{-1}. This suggested that D1 synthesis in *Z. capricorni* is not used in photoprotection and is not proportional to irradiance.

Ultra-violet radiation (280–400 nm) has been found to have substantial impacts on seagrasses (Larkum and Wood 1993; Dawson and Dennison 1996; Figueroa et al. 2002). Deep-water seagrasses are not acclimated to UV radiation and therefore are most sensitive. Shallow water seagrasses tolerate UV radiation. Larkum and Wood (1993) suggested the primary impact of UV-B (280–320) on *P. australis* was the oxidizing side of PSII, as it is in cyanobacteria and terrestrial plants (Vass et al., 2000; Larkum et al., 2001). Dawson and Dennison (1996) found *H. ovalis* and *Halodule uninervis* to be the most sensitive species to UV radiation. Thick-tissued species (*Z. capricorni, C. serrulate and Syringodium isoetifolium*) were only marginally impacted by elevated UV irradiance. UV has been shown to effect the $\Delta F/F_m{}'$, ETR_{max} and light-limited slope of the RLC (α). It has also been suggested that UV can affect down-regulation, as well as photoinhibitory sites (Figueroa et al., 2002).

G. Low Light Stress

Several investigations have examined the effect of light starvation, or more specifically, how shading limits seagrass distribution (Longstaff et al., 1999). Once a seagrass receives, at its midday maximum, less than 100–500 μmol photons m^{-2} s^{-1} (5–25% of surface irradiance), its respiration demands exceeds the rate of carbon fixation (Abal et al., 1994). When most of the downwelling irradiance is absorbed by the overlying water column, as well as increased scattering of light by suspended particles, this results in seagrasses being exposed to extreme shaded conditions (see Zimmerman, Chapter 13). In theory, low-light acclimation could be effected in seagrasses, by maintenance of a large population of inactivated PSII reaction centres. The advantage would be that these inactivated centres could function as effective energy quenchers of trapped light energy in fluctuating light climates. This would lower effective quantum yield, yet prevent photoinhibitory damage (Ralph, 1999). In a green alga, Longstaff et al. (1999) showed that chlorophyll pigment content responded rapidly to changes in the available light, which provided appropriate configuration of the light harvesting complex (LHC) to maintain photon capture at near optimal levels. Photochemical efficiency (F_v/F_m) was not effected during light starvation, as pigment adjusted to ensure maximum efficiency.

Major and Dunton (2002) investigated photoacclimation in *Thalassia testudinum* using PAM fluorescence and other techniques. Maximum quantum yield (F_m) was found to be elevated in low-light plants relative to high light plants, which were found to have increased F_o. They developed a model of seagrass photo-acclimation, based on light harvesting capacity optimised to lower irradiance, resulting in a reduction of P_{max} (light-saturated photosynthesis). Light harvesting was thought to increase by increasing chlorophyll content, thereby increasing the absorption cross-section and the efficiency of PSII (F_v/F_m) (Major and Dunton 2002). However, when leaf absorptance is maximized, increasing chlorophyll content has no effect on light harvesting. Thus leaves with low chlorophyll levels may modulate light harvesting by changing chlorophyll content, highly pigmented leaves cannot.

Several important questions still require further research; these include understanding the process of low light stress linked to increased turbidity, and shading by surface structures such as docks and excess shading by epiphytes as a result of eutrophication (Borowitzka et al., Chapter 19; Ralph et al., Chapter 24).

H. Photosynthetic Light Climate along the Leaf

Scale is an important consideration in all assessments of primary productivity. Photosynthesis is often used as a surrogate for assessing primary productivity, and photosynthesis varies across scales from the upper edge of an intertidal meadow to the deepest growing edge (Major and Dunton 2002). There is also variation in photosynthesis among individual plants, and we are now recognizing that there is variation in photosynthesis along a single leaf blade. The density of a seagrass meadow can cause self-shading, which will also influence the photosynthesis of a leaf (Enríquez et al., 2002). Durako and Kunzelman (2002) examined shoot-to-landscape scaling. Shoot-scale variation was assessed which included both within shoot, and between shoot variation. The youngest leaf of a *T. testudinum* plant was found to have the lowest F_v/F_m, while leaves ranked 2 (second oldest leaf) and 3, had higher F_v/F_m. Light-adapted maximum fluorescence (F'_m) decreased towards the tip of the leaf, indicating an increase in NPQ with higher light exposure.

Seagrass leaf blades can remain attached for over 6 months, causing gradual changes in light climate as the leaf moves through different vertical positions and acquires different degrees of epiphytic cover. The age of a leaf blade strongly influences its photokinetic responses (Enriquez et al., 2002). Several investigations have recognised that photosynthesis is not constant along a leaf (Ralph and Gademann, 1999; Durako and Kunzelman, 2002; Enríquez et al., 2002). Since seagrasses grow from the basal meristem, this region has the least chlorophyll and also receives the least incident irradiance (Enriquez et al., 2002). As the leaf ages, each section moves progressively to higher light climates, so cells within a leaf must be shade acclimated initially, then progressively photo-acclimated to higher light (Zimmerman, Chapter 13). Enríquez et al. (2002) found that sections of a leaf can experience a wide range of irradiance, which can change by three orders of magnitude over the leaf's lifetime. Enríquez et al. (2002) examined age-dependent loss of F_v/F_m in *T. testudinum*. From the base to about 4 cm, maximum quantum yield increased, and then gradually declined possibly due to exposure to irradiances about saturation. RLCs of *P. australis* showed three regions of distinct photochemical patterns along a leaf: the basal region (2–4 cm) with low ETR, E_k and high F_v/F_m; middle region (8–22 cm) with higher ETR, E_k and F_v/F_m; and finally the apical region with the highest ETR, E_k and F_v/F_m. This shows a gradation in photokinetics along a leaf blade (Ralph and Gademann 1999). In contrast, Ralph et al. (2002) found that F_v/F_m, qP and NPQ did not vary along *Z. marina* leaf blades, which was confirmed by constant levels of xanthophyll and carotenoid pigment; whereas, for *T. testudinum* the F_v/F_m ratio declines at a rate of 1.5% cm^{-1} along the blade (Enríquez et al. (2002)). This gradation was attributed to down-regulation occurring in the 4–8 cm region, whilst photodamage (photoinhibition) occurred in section >11 cm from the meristem. Treatment with chloramphenicol confirmed that the apical region had limited capacity for protein synthesis during high light exposure.

Another way to study photosynthetic effects by fluorescence, apart from PAM fluorometry, is to study the so-called O-J-I-P fluorescence rise kinetics, i.e. the initial rise in fluorescence upon turning on actinic light. In theory, the O-J-I-P polyphasic transients can be used to follow the sequential reduction of PSII internal electron acceptors. Enríquez et al. (2002) studied fluorescence rise kinetics in *T. testudinum* using the Hansatech PEA fluorometer. It was found that apical regions had an elevated J transient, which was taken to indicate a decrease in the Q_A^- reoxidation capacity of these older sections of the leaf. This is one characteristic of photoinhibition, where, in contrast to UV-B inhibition, the acceptor side of PSII is inhibited; however, it could also be linked to non-photochemical quenching (a photoprotective mechanism). The powerful tool of fluorescence induction will undoubtedly provide insights into the dynamic processes of photosynthesis. However, more work is needed to address its use in seagrasses.

I. Comparison of Fluorescence and O_2 Evolution-Derived Rates of Photosynthesis

Fluorescence measures only photon-driven electron transport through PSII, which should be linearly correlated with O_2 evolution. It should also be directly correlated with the rate of photosynthesis, since $NADP^+$ reduction depends on linear electron transport through PSII and then PSI. However, both electron transport and oxygen exchange are complicated by several competing processes, including cyclic electron transport within PSII, photorespiration and the Mehler Ascorbate Peroxidase (MAP; O_2-consuming) pathway (Fig. 2). Therefore, chlorophyll *a* fluorescence techniques cannot easily be compared with O_2 evolution. *C. nodosa* and *H. ovalis*, have been shown to have a linear relationship between ETR and O_2 evolution (Beer et al., 1998, Beer and Björk, 2000). However, it is more common for a curvilinear relationship to exist between photosynthesis as estimated by fluorescence and oxygen-evolution techniques (Beer et al. 1998; Ralph and Burchett, 1995; Beer and Björk, 2000).

In algae, where these two techniques have been widely compared, it has been shown that there is probably a cycle of electrons around PSII under high irradiances (Franklin and Badger, 2001; Longstaff et al., 1999) and therefore PAM-derived ETRs only correlate with O_2-derived rates at low to moderate irradiances (Longstaff et al., 2002). The relationship becomes increasingly non-linear at irradiances above saturation. Above saturation, a range of possible uncoupling processes may be influencing this response such as photorespiration, MAP pathway reactions and photoinhibition (Fig. 2). Photorespiration has been suggested as causing the divergence from linearity for several species *H. stipulacea* and *Z. marina*. On the other hand *C. nodosa* showed a linear response and it was suggested that this seagrass may have developed a carbon concentration mechanism (Beer et al. 1998). However, it likely that most seagrasses have a CCM mechanism (Section IV) and thus some other factor would have to be invoked. The MAP pathway is largely unexplored in seagrasses (see section VII) which is regrettable since, with the high O_2 levels generated due to the deep diffusion boundary layers at the seagrass leaf surface, high activity of this pathway might be predicted (Miyake and Asada 2003). Thus, the results from seagrasses appear to mirror those found for algae (above) indicating more research is needed to detail the mechanisms involved in the non-linearity between oxygen and fluorescence in seagrasses.

Perhaps the critical limitation of correlating fluorescence and oxygen evolution is the assessment of the light absorption by the leaf, which is fundamental in deriving ETR from PAM data. Beer et al. (1998) recommended that a more accurate method of estimating the absorptance should be found. Numerous attempts have been made to estimate the absorption of light (Enríquez, et al., 1992) (as well as reflection and transmission); however, until recently no single method has provided an adequate estimate (eg. see Beer and Björk, 2000). Schwarz and Hellblom (2002) recently demonstrated that the fraction of absorbed light varies with depth, therefore questioning the merit of accurately determining the absorption for each species if it also needs to correct for depth. A new instrument called the Imaging-PAM (Walz Effeltrich, Germany) has the capacity to measure absorbtivity, where the relative absorption of red

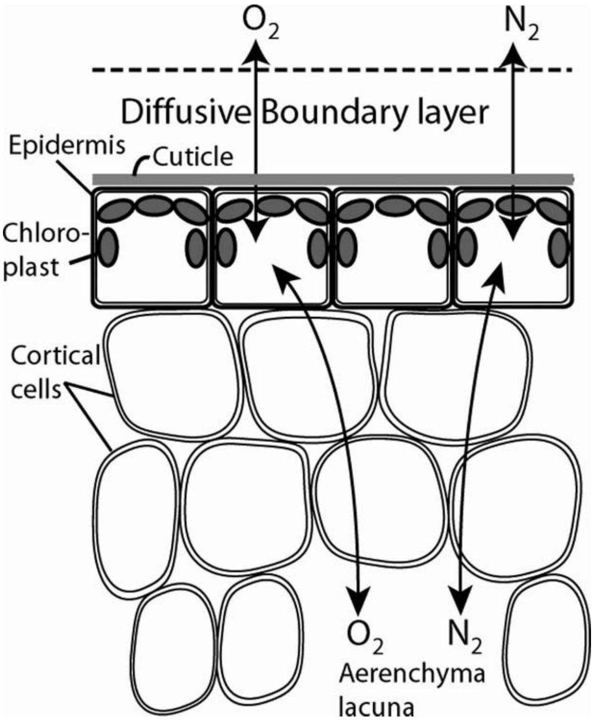

Fig. 4. The pathways of gaseous movement in the photosynthetic and aerenchymal tissue of seagrass leaves.

light is compared to near-infrared light, thus providing an estimate of photon absorption (Ralph et al., 2005). Unfortunately, this instrument cannot address the issue of differential light absorption between two photosystems that is linked to state transitions. State transitions are the fluorescence transients that occur when light that stimulates PSI or PSII differentially is applied (a situation that can easily occur in fluorescence techniques where red or blue light emitting diodes are used to supply actinic light). Fortunately state transitions are relatively small in higher plants compared with algae (Larkum, 2003).

IX. Leaf Anatomy, Oxygen Effects and Depth Limitations in Seagrasses

The anatomy of seagrass leaves involves an aerenchyma to a greater or lesser degree. Because of the large DBL around the leaves a natural consequence is that O_2 liberated in photosynthesis accumulates in the air spaces under pressure rather than diffusing out into the ambient seawater. However, there is only a limited capacity for the airspace system to absorb this influx of O_2 (<10 min at typical P_{max}) after which the major route is efflux of O_2 through the leaf surface (Larkum et al., 1989) (Fig. 4). As a result the local concentrations of O_2 in chloroplasts in the light must are be very high (Borum et al., Chapter 10) and the consequences of which this are poorly understood. Oxygen is a very reactive species at the best of times and in very high concentrations must be even more reactive. One expression of this must be the production of singlet oxygen by PSII, causing degradation of D1 protein and the impairment of overall PSII activity (Andersson and Aro, 2001; Section VIII.F). We have already discussed the possibility of offsetting the damage of high O_2 by the deployment of three processes (i) photorespiration, (ii) the MAP pathway and (iii) electron cycling in PSII. A fourth process is down-regulation of photon energy before it gets to PSII by the xanthophyll cycle (Section VIII.E). Suffice it to say that none of these processes is well studied in seagrasses and at present these matters are wide open for debate.

Pressure change in seagrasses (Borum et al., Chapter 10) was invoked as a major reason for the fact that seagrasses penetrate to lesser depths than algae (Beer and Waisel, 1982). However, two other reasons can be adduced for such a limitation. One is the strong dependence on a non-photosynthetic rhizome/root system in seagrasses, which reduces the overall primary production of the plant and reduces the compensation depth. The second is that light harvesting in seagrasses is strongly dependent on excess chlorophyll proteins (Section VI), whereas algae have a much greater range of more efficient light-harvesting strategies. Anatomical and morphological factors in depth limitation are discussed are discussed in Kuo and den Hartog, Chapter 3.

Duarte (1991) found that the differences in the depth limits of seagrasses were largely attributable to differences in light attenuation and could be described by a fairly simple equation:

$$\mathrm{Log} Z_c = 0.26 - 1.07 \log \mathrm{K}$$

Where Z_c is the depth limit of a seagrass (m) and K is the underwater light attenuation (m^{-1}). As discussed in Section VI, while the non-photosynthetic parts of seagrasses probably impose on them a shallower depth limit as compared to algae, there are probably a range of morphological types involved, from the heavy investment in roots and rhizomes of species like *P. oceanica* and *P. australis*, to the much reduced investment in species like *H. ovalis* and *H. capricorni*. This is probably reflected in the much greater depth limits of the latter species (Duarte, 1991). Olesen et al. (2002) compared changes in anatomy, physiology and growth characteristics (population structure) with depth in the co-occurring *P. oceanica* and *C. nodosa*. *C. nodosa* showed the greatest flexibility and reduced its below-ground parts and increased its leaf area. However, photosynthetic efficiency at low PAR was about the same for each species. *P. oceanica* was able to survive longer at low irradiance due to low growth and low respiratory rates. The greatest depth range of any seagrass is ~90 m (*H. capricorni*) which represents ~11% of surface irradiance (in clear oceanic waters) (Duarte, 1991). For phytoplankton the limit is generally held to be 100 m or 1% of surface irradiance, although the record is held by a coralline red macroalga (Littler et al. 1995) at 268m m, where the light was 0.0005% of surface irradiance.

X. Initial Photosynthetic Products in Seagrass Leaves

By far the largest proportion of carbon fixed photosynthetically by seagrass leaves is rapidly accumulated in the ethanol soluble fraction, primarily as the disaccharide sucrose (see Fig. 5). After only 5 minutes incubation with ^{14}C-bicarbonate, over 50% was incorporated into sucrose and neutral amino acids in the tropical seagrasses, *H. spinulosa* and *T. hemprichii* (Andrews & Abel, 1979). In a survey of six tropical and temperate species reported by Abel & Drew (1989), the major ^{14}C labelled product after 1 hour was always sucrose in *C. nodosa, C rotundata, Phyllospadix torreyi* and *Thalassodendron ciliatum* or its constituent monosaccharides glucose and fructose in *H. uninervis* and *S. isoetifolium*. In a more detailed study of *C. nodosa,* Drew (1983) found that after 1 hour 97% of photosynthetically fixed ^{14}C was in the ethanol-soluble fraction, mostly as sucrose (89.2%) plus 6.2% as glucose and 2.1% as fructose.

XI. Translocation and Exudation

Few direct measurements of the movement of photosynthetically fixed carbon within seagrass plants have been reported. Harrison (1978) showed that, during a 3 hour incubation, 6.5% of the ^{14}C fixed by vegetative shoots of *Zostera americana* moved to rhizomes and other shoots, but only 1.6% moved from flowering shoots. The terminal shoot and any flowering shoots present on the rhizome were the major sinks for this translocated carbon. Drew (unpublished) found that 2.5% of the carbon fixed by leafy shoots of *P. oceanica* was translocated from the green leaf tissue during a 4.3 hour incubation (Fig. 5). Only one third of that passed beyond the unpigmented leaf sheaths into the rhizomes and there was a lag of 2 hours before any significant movement was detected.

Exudation was not measured in the experiments of either Harrison or Drew. However, Wetzel and Penhale (1979) showed that when ^{14}C was fixed in the roots of *Zostera marina* during a 4 hr incubation, most accumulated in the leaves (82.4%) and a small amount of dissolved organic carbon (DOC) was lost from the leaves (0.15%). The situation in *T. testudinum* was similar, with 97.7% being fixed in the leaves and epiphytes and 1.4% lost as DOC. This was similar to the 1.3% of gross fixation, which Brylinsky (1977) found to be released from T. *testudinum* to the surrounding medium. *H. wrightii* (Brylinsky, 1977) and *C. serrulata* (Birch, pers comm) are also known to release organic carbon to the medium and the photorespiratory product

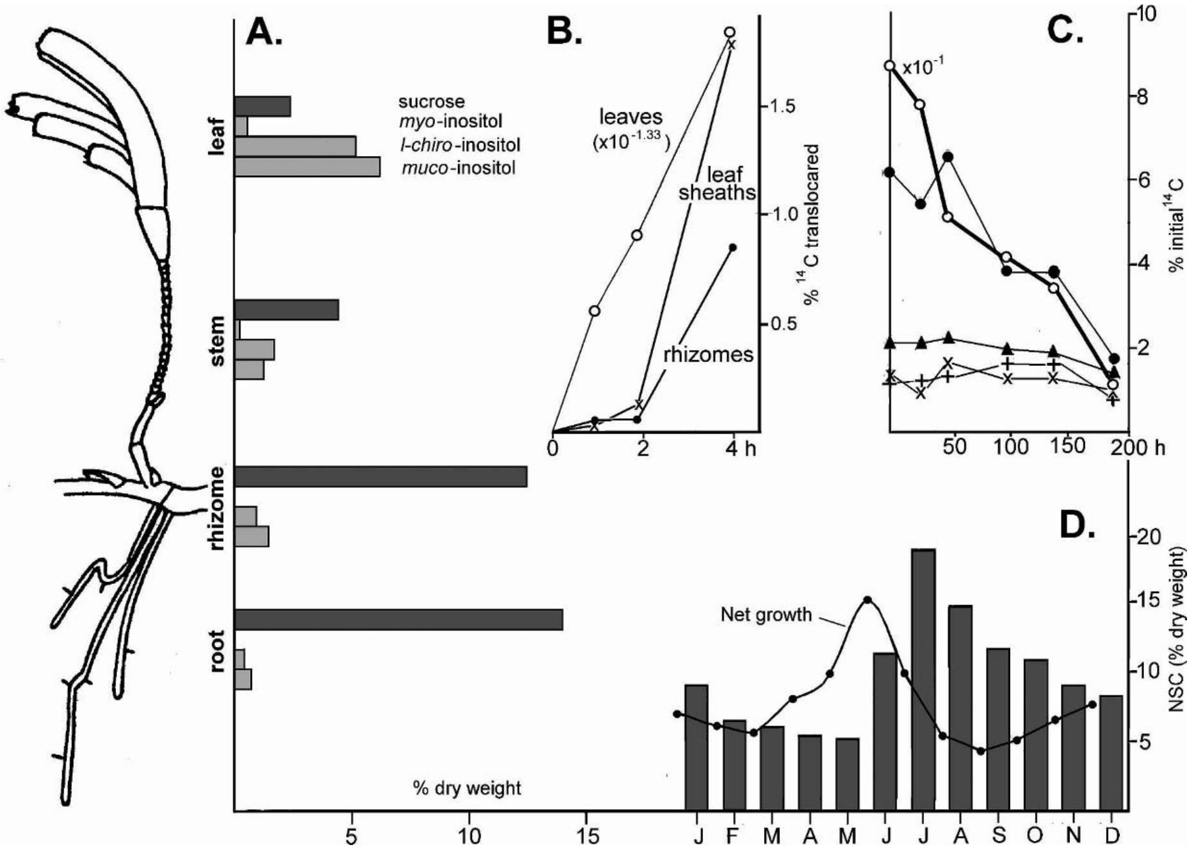

Fig. 5. (A) Changes in sucrose and inositol content from leaves to roots of *Thalassodendron ciliatum*. Redrawn from Drew (1978)
(B) Translocation of photosynthetically fixed carbon within *Posidonia oceanica* during 4.3 h (Redrawn from Abel & Drew, 1989
(C) Distribution of ^{14}C in *Cymodocea nodosa* after 1 h photosynthesis, and subsequent utilisation in the dark over 200 h (Redrawn from Drew, 1978)
(D) Seasonal changes in non-structural carbohydrates (as sucrose-equivalents) in *Posidonia oceanica*, compared with plant growth rates (Redrawn from Alcoverro et al., 2001).

glycolate is released from at least two seagrasses, *T. hemprichii* and *H. ovalis* (Fogg, 1976). Jorgensen et al. (1981) have demonstrated release of significant amounts of amino acids to both the overlying water column and sediment pore-waters by *P. oceanica* and C. *nodosa* in the Mediterranean. A major part of the exudation quantified above may also be as amino acids, and in addition to involvement in nitrogen recycling, may act as a chemo-attractant for rhizoplane bacteria (Wood and Hayasaka, 1981).

XII. Storage and Utilisation

Significant movement of photosynthetic products within seagrass plants is also shown by the relatively high concentrations of non-structural carbohydrate carbon (NSCC), which can accumulate, in the underground structures (Fig. 5). On the basis of 24 reported studies involving 18 seagrass species from 10 genera, Touchette & Burkholder (2000) concluded that average soluble carbohydrate levels are 10% dry weight in leaves, 9.5% in stems, 27.5% in rhizomes and 13.5% in roots. Storage of carbohydrate reserves in below-ground structures will protect them from herbivory and also ensures adequate reserves are available to sustain the perennating structures during dormant periods. In addition to sugars, particularly sucrose, starch can represent a considerable proportion of the carbohydrate reserves. In *Z. noltii* this can approach one third of total NSCC (Pirc, 1989; Vermatt & Verhagen, 1996), although Peralta et al. (2002) report that starch levels did not exceed 0.4% dry weight compared with up 25% dry weight sucrose in the same species. Starch may represent up to two thirds of total NSCC in *Z. marina* carbohydrates (Burke et al., 1996), and up to 90% in leaf and root tissue of *H. ovalis* (Longstaff et al., 1999). In *Z. marina* sucrose mobilisation in roots is stimulated by low-light conditions in winter and translocation to the shoots is inhibited by anoxic conditions (Zimmerman et al. 1995; Alcoverro et al., 1999).

Marked seasonal changes in NSCC reserves have been documented in several seagrasses). Alcoverro et al. (2001) report minimum levels from February to May in *P. oceanica* when the plants were growing rapidly under conditions of high dissolved nutrients and increasing irradiance and day length, followed by rapid accumulation in summer when nutrients had become exhausted but irradiance levels were still high (Fig. 5D). These reserves were then slowly depleted until the following spring. Vermaat & Verhagen (1996) also report a strong increase in rhizome sugar content in July when growth had largely ceased but photosynthetic capacity was still maximal. Lazar & Dawes (1991) found the same trend in *Ruppia maritima.* Blade growth in that species occurred in winter, even earlier than in *P. oceanica*, and high levels of soluble carbohydrates (26.7 to 52% dry weight) did not accumulate until spring and early summer after blade production was completed but before they died back in late summer and autumn.

Clearly seagrasses have a wide variety of metabolic pathways, such as those of cell wall synthesis, and these involve a variety of sugars such as arabinose, fucose, galactose, mannose, rhamnose and xylulose (Waldron et al., 1989; Webster and Stone, 1994).

XIII. Secondary Metabolites and Chemotaxonomy

In addition to the ubiquitous sucrose, glucose and fructose, plus two trisaccharides apparently restricted to *Phyllospadix* spp., several seagrasses accumulate considerable amounts of another type of soluble carbohydrate, inositols. Of the nine possible inositols, only 5 are known to occur in plants and only *myo-, l-chiro-, muco-* and an *0-methyl-muco*-inositol occur in seagrasses. Drew (1984) reviewed current knowledge of the possible roles of the inositols and their several methyl esters found in plants: their restricted distribution shows significant taxonomic correlations.

Myo-inositol is found in all living cells in amounts usually considerably less than 1% dry weight. It is apparently synthesised by direct cyclization of photosynthetically-produced glucose (Loewus & Kelly, 1962) and is then involved mainly in cell wall synthesis (Loewus, 1965). Leaves and rhizomes of some seagrasses, particularly the Zosteraceae, contain relatively large amounts of this compound, up to a maximum of 2.2% dry weight in *Z. noltii* rhizomes.

In most plants the cyclization enzyme is conservative and yields only *myo*-inositol, which then acts as the sole precursor for any other inositols they accumulate. Drew (1978, 1983) suggested that, since the configuration of the glucose molecule would permit the direct formation during cyclization of all the inositols found in seagrasses, they may be inevitable by-products of another, less specific, glucose cyclization enzyme. Only members of the predominantly tropical zannichelliacean seagrasses (Cymodoceaceae) accumulate these other inositols, with a preponderance of *l-chiro*-inositol. This compound has been detected in all genera except *Halodule,* with a maximum of 6.8% dry weight in *C. rotundata* leaves. *Muco*-inositol appears to be slightly less widely distributed in these seagrasses whilst its *O-methyl* ester is restricted to the endemic temperate Australian genus *Amphibolis.*

Drew (1978) showed that in *C. nodosa* photosynthetically-fixed ^{14}C was incorporated only slowly into these unusual compounds with 1.3% of soluble ^{14}C in *myo*-inositol and 1.1% in *l-chiro*-inositol after 1 hour. However, those other than *myo*-inositol can probably accumulate to several percent dry weight because they are not subsequently utilised even after all soluble sugars have been respired away during dark starvation for several days.

The possibility that these compounds might be involved in an osmoregulatory role was not supported by studies at high and low salinities (Drew, 1978) although respiration, and therefore sucrose utilisation was increased at both extremes. Tyerman et al. (1984) also implicated sucrose, and possibly amino acids, as minor osmoregulants in their study of the osmotic environment of *P. australis* leaves. Proline, an amino acid frequently involved in osmoregulation in halophytes, has been found to increase with increasing salinity in *Halodule wrightii, Ruppia maritima* and *Thalassia testudinum* (Pulich, 1986). Alanine increased similarly in *H. engelmanni* (Pulich, 1986). In *P. australis* and P. *oceanica* these amino acids occur only at low levels (Augier, 1982).

Tyerman (1989) presented evidence that sucrose serves an osmoregulatory role as a compatible solute in the cytoplasm of *Zostera capricorni* and the same may be true for *P. australis* (Tyerman et al., 1984).

These are the only reports to date on the possible involvement of organic compounds in seagrass osmoregulation. However, the presence of considerable quantities of various inositol derivatives in mangroves (Popp, 1984) suggests that this diverse group of plants growing exclusively in wet, saline environments, similar to those of the seagrasses, may use these unusual compounds to alleviate their considerable osmoregulatory problems.

Several types of secondary metabolites have been studied in seagrasses, usually from a chemotaxonomic viewpoint. Attaway et al. (1970) found that the normal alkanes of several genera represented less than 0.01% dry weight but their distribution paralleled current taxonomic schemes of the seagrasses with *Halodule (Diplanthera)* and *Syringodium* distinguished from each other and even more clearly from *Thalassia* and *Halophila.* Both groups were very distinct from *Ruppia.* Cluster analysis of high-resolution GCMS analyses of the sterols and fatty acids of a number of species from tropical Australia (Gillan et al., 1984) also confirmed significant segregation of the zannichelliacean genera *Cymodocea* and *Halodule* from the hydrocharitacean genera *Thalassia* and *Enhalus.* However, *Halophila,* a genus from the latter family but with very different morphology, was separated at a much higher level from all the other seagrasses analysed. That study was aimed at tracing seagrass-derived material throughout the coastal ecosystem. A similar approach in temperate Australia by Nicholls et al. (1982) showed that the lipids, comprising up to 7.6% dry weight, of *P. australis* and *Heterozostera tasmanica,* had patterns of monocarboxylic, dicarboxylic and hydroxy acids sufficiently different to allow even detritus of these two species to be distinguished.

Taxonomic questions at the species level in seagrasses have also been approached chemically by McMillan et al. (1981) and McMillan (1983) using secondary products such as the flavonones and their sulphonated derivatives from *Amphibolis, Halodule, Halophila, Posidonia* and *Zostera.*

XIV. Summary

Photosynthesis in seagrasses is constrained by their aquatic existence. Apart from living in seawater, with its high ion concentrations (the effect of which on photosynthesis is little known) seagrasses share many of the same features as freshwater hydrophytes. The most influential effect, on photosynthesis, is the diffusive boundary layer and the limitations it imposes on the uptake of C_i. As suggested by Maberly and Madsen (2002), many of the unique features of aquatic plants originate from adaptations to overcome these limitations. In hydrophytes the adaptations which occur are (i) obtaining CO_2 directly from the sediment via roots (well documented in some freshwater hydrophytes, but not in seagrasses), (ii) possessing the ability to undertake CAM or C_4-like metabolism and, most common of all, (iii), being able to exploit reserves of HCO_3^-, as well as accessing atmospheric CO_2 (a device large denied to seagrasses). Aerenchyma is also a shared feature with freshwater aquatics as an adaptation to reduce respiratory load (Williams and Barber, 1961) and to carry oxygen to underground parts and CO_2 to the leaves (see Borum et al., Chapter 10). Although photosynthesis can contribute only small amounts of gas exchange to the aerenchyma system (the major pathways of exchange of C_i and O_2 being across the epidermis), it nevertheless has a powerful effect on pressurising the aerenchymal system. The effects of this pressurisation on photosynthesis and other physiological processes have been little studied.

Fluorescence techniques are currently providing a powerful tool for studying photosynthesis *in situ*, and this will be a much-needed impetus to study, since seagrasses in contrast to freshwater aquatics cannot easily be studied in tank cultures. First of all there is a need to carry out detailed comparisons on the relationship between rates measured by other techniques (e.g. O_2 evolution) and fluorescence techniques. Then there are a host of individual questions to be asked and answered, such as the effect of flow, the position along the leaf, the operation of the xanthophyll cycle in photoprotection, and the influence of a changing spectral light climate through the canopy on photosynthesis (Zimmerman, Chapter 13) and other influences on light harvesting processes. In this regard the recent addition of the Imaging PAM should have a marked effect in speeding up this area of research.

In terms of the biochemistry of photosynthesis, it is clear that there is much still to be done and that seagrass research in this area has lagged behind that in freshwater aquatics. The roles of β-carboxylation, MAP and photorespiration deserve renewed investigation, as do the processes of sugar metabolism and export from the leaves. Finally the area of secondary metabolites and the role of such products as myo-inositols is an intriguing one, which has received almost no research over the last decade.

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Chapter 15

Remote Sensing of Seagrass Ecosystems: Use of Spaceborne and Airborne Sensors

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I. Introduction

A. Remote Sensing and Aerial Photographic Approaches

The focus of this chapter lies in describing digital multispectral and hyperspectral remote sensing developments and applications in the mapping and monitoring of seagrass ecosystems. Multispectral refers to a sensor that registers light in a limited number of relatively broad spectral bands (bandwidths of 20–60 nm); hyperspectral (also referred to as imaging spectrometry) is defined for sensors that measure the entire spectrum under consideration in contiguous narrow spectral bands (bandwidths between 2 and 20 nm).

Currently, seagrass maps are still predominantly being produced from the interpretation of aerial photography although it is likely that airborne and spaceborne remote sensing methods will rapidly take over this role given the advantages they present in terms of accuracy, repeatability, versatility, and information content. Nevertheless, retrospective studies of seagrass change using the more modern methodologies will still need to make use of results generated by the more traditional methods since aerial photographs are the dominant archival source of historical spatial information on seagrass meadows. The subject of aerial photography and the assessment of seagrass vegetation has been extensively dealt with in Global Seagrass Research Methods (Short and Coles, 2001) and the reader is referred to reviews in that publication, as well as to relevant sections of Green and Short (2003).

Traditional satellite sensors offer a cost-effective approach for mapping seagrass over large areas and in remote locations (Ferguson and Korfmacher, 1997; Mumby et al., 1999) particularly where the meadows are large, monospecific, and continuous. The value of the repeated temporal cover provided by satellite sensors has been shown by Jensen and coworkers who investigated the application of Landsat MSS and SPOT multitemporal data to successfully evaluate change in cattail and seagrass species in the Everglades (Jensen et al., 1995). Multi-date satellite remote sensing is geometrically highly repeatable and a cost-effective method for detecting large changes in seagrass distribution or extent over time (Robblee et al., 1991; Zainal et al., 1993; Ward et al., 1996; Macleod and Congalton, 1998). Anstee et al. (2004) detected seagrass and macro-algae change in a shallow coastal tidal lake in Australia using archival Landsat satellite image data from 1988 to 2002, by applying hyperspectral measurement and modeling techniques to the multispectral Landsat images. They were able to determine that *Posidonia*

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australis cover remained stable whilst *Ruppia* sp. and *Halophila* sp. cover varied slightly. The most significant change had occurred in the cover of *Zostera capricorni*, which had been replaced by cover of macro-algae species like *Chara* and *Nitella* or the *Zostera* had been overgrown by dense epiphytes.

B. Recent Advances in Remote Sensing

Satellite remote sensing technology changed dramatically at the end of the 1990s: very high spatial resolution sensors such as IKONOS and QuickBird became available, offering pixel sizes of 0.6–1.0 m in panchromatic and 2.4–4 m in the multispectral bands. In addition, a new generation of satellite systems that build on the Landsat and SPOT series were launched, providing intermediate ground resolution of between 5 and 25 m, an increased number of spectral bands and higher radiometric sensitivity. These systems include Landsat 7 TM, SPOT 5, and ASTER. Sensors with increased spatial resolution will better suit the discrimination of small and patchy, or narrow, linear seagrass beds that commonly occur in small estuaries but they may not improve the accuracy of mapping large seagrass meadows (e.g. Mumby and Edwards, 2002; Malthus and Karpouzli, 2003). However, because of the wide range of satellite sensors now available, imagery can be selected to match the scale and objective of almost any seagrass mapping project.

Multispectral sensors mounted on aircraft became available in the early 1980s, followed by hyperspectral sensors in the mid-1980s. At first these were mainly research-type instruments, but from the early 1990s onwards, commercial companies provided instruments such as the CASI and the HyMap. Many other hyperspectral instruments were also developed, but since they were usually custom-built they were never capable of generating multiple use. However, the capabilities of these new airborne instruments and the potential they offered were the main driving force behind research and development of quantitative hyperspectral measurement and modeling-based, methods for mapping seagrass and associated ecosystems.

Increasingly, results detailing the high spectral resolution reflectance properties of submerged aquatic vegetation and associated substrata in situ are being published. Reported spectra for a range of species and growth habits, mainly for assessing the potential for their spectral discrimination in remote sensing images are reported (Malthus and George, 1997; Alberotanza et al., 1999; Myers et al., 1999; Hochberg and Atkinson, 2000; Lubin et al., 2001; Fyfe, 2003; Kutser et al., 2003; Anstee et al., 2004; Karpouzli et al., 2004).

C. Imaging Seagrass Beds

A number of researchers have investigated the application of airborne hyperspectral or multispectral digital sensors for discriminating and mapping benthic plant species (e.g. Zacharias et al., 1992; Bajjouk et al., 1996; Clark et al., 1997; Malthus and George, 1997; Mumby et al., 1997a; Thomson et al., 1998; Alberotanza et al., 1999; Pasqualini et al., 2001) and for estimating seagrass biomass (Mumby et al., 1997b). Many recent studies into light in shallow waters and hyperspectral (modeled, in situ measured and from airborne systems) mapping of seagrasses, macro-algae, benthic micro-algae and coral reef species are documented in *Limnology* and *Oceanography* (2003) Volume 48.

The principle of the use of airborne imaging spectrometry for measuring the subsurface reflectance $R(0-)$ (see Eqs. (11–13)) over a water body with seagrass is presented in Fig. 1. A CASI image over a shallow coastal water body near Adelaide (Australia) was corrected for atmospheric and water column effects using radiative transfer (RT) models. Simultaneous in situ measurements of benthic reflectance of *Posidonia australis* were collected using a field spectrometer at the time of aircraft overpass. Fig. 1 compares the results of Hydrolight-based modeling of at surface reflectance spectra of *Posidonia P. australis* under different depths of a water column with atmospherically corrected CASI image spectra from the shallow water site where *P. australis* was measured. The relevance of this work is that a spectrum measured by a remote sensor can increasingly

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Abbreviations: ASTER – advanced spaceborne thermal emission and reflection radiometer; CASI – compact airborne spectrographic imager; CDOM – colored dissolved organic matter; HyMap – series of airborne hyperspectral sensors; IKONOS – a high spatial resolution multispectral satellite sensor; Landsat – a series of land imaging satellites from 1984 to present; Landsat 7 TM – the most recent Landsat sensor: Landsat Thematic Mapper 7; QuickBird – a high spatial resolution multispectral satellite sensor; SPOT – systeme probatoir d'observation de la Terre: Satellite sensor system from 1984 to present; SPOT 5 – sensor nr 5 of SPOT; RT – radiative transfer of energy theory. Note: for symbols on light in the sea, see Chapters 12 and 13.

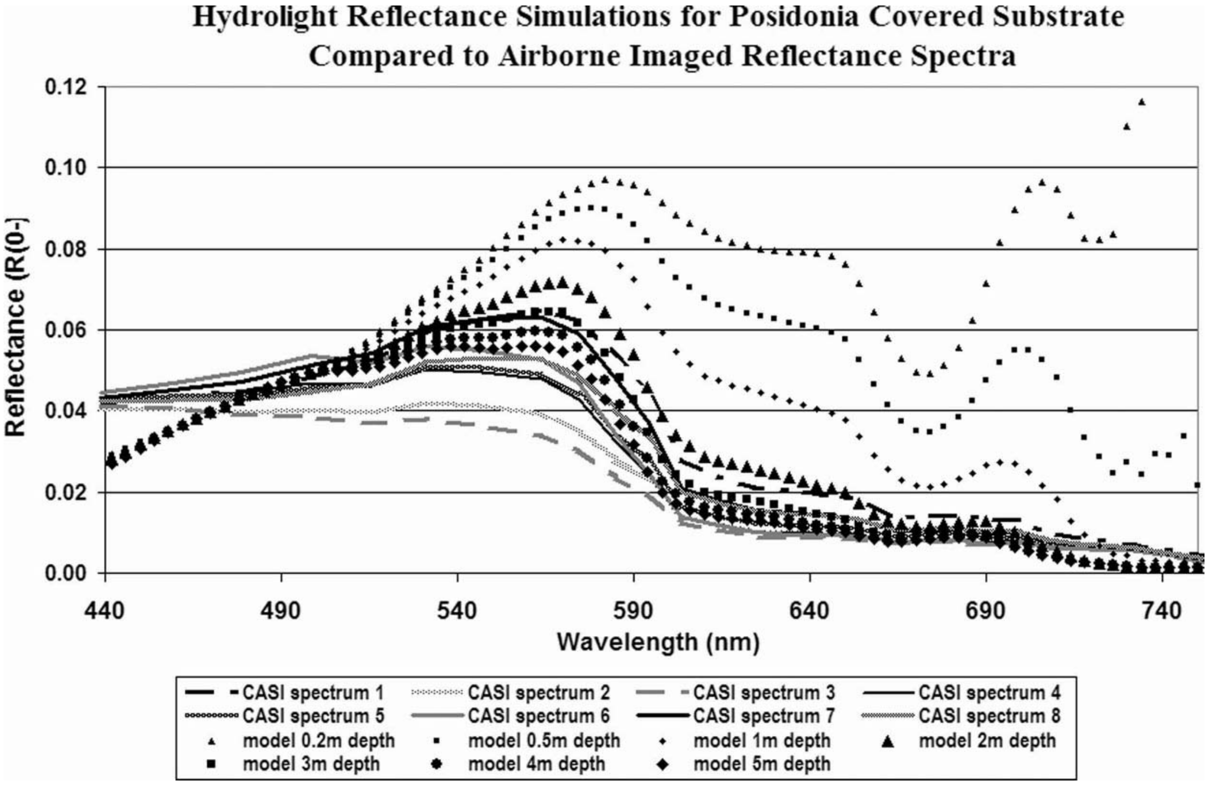

Fig. 1. Modeled $R(0-)$ *Posidonia australis* spectra at different depths in the water column compared to some mean class spectra derived from the CASI image $R(0-)$ of the Bolivar test site near Adelaide (Australia) in 2001. *P. australis* spectra match well with CASI spectra for depths between 2 and 5 m. The modeled $R(0-)$ spectra are only lower for the shorter wavelength region between 450 and 490 nm. The differences in reflectance in this blue region could depend on: the low blue light sensitivity of the CASI sensor, the residual errors in the CASI atmospheric correction or the possible errors in the inputs into the Hydrolight simulations.

be simulated accurately by RT modeling. Inverting these methods can provide more accurate assessments of the water composition, the depth, and the substratum including benthic vegetation cover.

The results of spectral studies, light interaction studies in seagrass canopies (see Chapter 13), and remote sensing image classifications suggest that high resolution remote sensing systems may provide detailed maps of benthic species and/or habitats, as well as information on the biophysical and possibly physiological condition of the seagrasses (Fyfe, 2003). Airborne hyperspectral imagery provides the benefits of high spectral, spatial, and radiometric resolution with a high signal-to-noise ratio. Hyperspectral data give the user access to a variety of new discrimination and classification techniques since the narrow bandwidths enable spectral shapes to be utilized in seagrass pigment feature identification. The best results will be obtained from sensors with spectral bands adequate for species discrimination and capable of significant penetration into the water body to interact with the benthic vegetation. Airborne remote sensing can overcome the spatial limitations inherent in conventional satellite sensors for accurate monitoring of small-scale dynamics in seagrass meadows (<10 m ground resolution). While geometric accuracy and repeatability has been a problem for all airborne systems in the past, including aerial photography, new digital airborne sensors are equipped with increasingly more sophisticated instruments for on-board geometric and radiometric registration. In combination with automated post-flight correction software, this makes the image data more accessible to seagrass researchers or managers who are not remote sensing specialists.

For most coastal regions which support seagrass meadows, hyperspectral airborne sensor data provide significantly more biological information about the seagrasses, macro-algae, and possibly microphytobenthos than the conventional spaceborne sensors such as Landsat TM and SPOT (e.g. Mumby et al., 1997a, 1998; Jakubauskas et al., 2000) and is a geometrically accurate, cost-effective alternative to aerial photography (Mumby et al., 1997a).

II. Principles of Remote Sensing of Seagrass Ecosystems

The remote sensing of seagrasses and related seabed habitats is based on the principle that a remote sensor can 'see' the substratum and the vegetation growing on or in (microphytobenthos) that substratum. Seagrasses are covered by a water column that attenuates the light reaching, interacting with (see Chapter 13), and being reflected from the benthos. While the remote sensing of terrestrial plants makes significant use of the red edge (i.e. the steep slope between strong red wavelength absorption and strong near-infrared reflectance characteristic of the spectral signatures of healthy plant leaves), aquatic plants cannot be recognized by this feature since wavelengths beyond 680 nm are significantly attenuated by pure water (Kirk, 1994), beyond a water column depth of 1–2 m. In coastal waters, spectral scattering and absorption by phytoplankton, suspended organic and inorganic matter, and dissolved organic substances further restricts the light passing to the benthos (Dekker et al., 2001). Zimmerman (Chapter 13) discusses the effects of higher concentrations of optically active materials in the water column on seagrass photosynthesis. Spectral discrimination between aquatic plant species must therefore concentrate on pigment related spectral features within the visible wavelengths, where light penetrates the water column and can be reflected back to the sensor (Fyfe, 2003). Absolute reflectances from submerged species are generally low, often lower than the reflectance from a deep water column, and from a visual perspective seagrass areas generally appear darker than non-vegetated areas. One of the reasons for seagrasses generally appearing darker in remote sensing images and aerial photography is the shading that takes place within the canopy (see Chapter 13 for details).

In all physics-based applications where the substratum is mapped through a water column, a bathymetry estimate (i.e. a water column depth estimate) is implicitly or explicitly involved. Optically shallow waters are a special case in the remote sensing of aquatic systems. Under these conditions a measurable signal will be detected from the substratum or plants, through the water column and through the air–water interface. The water is considered to be optically deep if there is no measurable influence of the benthos or substratum on the remotely sensed reflectance (Dekker et al., 2001).

The bathymetry and the water column optical properties are thus important to remote sensing in aquatic environments, in particular for seagrass and macro-algal mapping (Dekker et al., 2001) since optimal results will be obtained from remote sensing if the signal from the seagrass canopy is maximized by compensating for the attenuating influence of the water column. Whether a benthic feature such as seagrass can actually be discriminated depends on the spectral optical depth of the water column (and the atmosphere between the sensor and the water surface), the brightness and density of the vegetation, and the spectral contrast between it and the substratum, as well as on the spectral, spatial, and radiometric sensitivity of the remote sensing instrument.

Remote sensing of aquatic environments (seagrass, sand, macro-algae, muds, and coral reefs) requires sensors with greater sensor signal-to-noise ratio than those applied in terrestrial environments. Coupled with this factor is the number of quantization levels to which the sensor can record, referred to as the radiometric resolution of the sensor. This must be high enough to allow a range of brightness levels over which a classification can be performed and sensitive enough to be able to detect the lower reflectance of the deeper seagrass beds (Dekker et al., 2001). Seagrasses may grow with sparse cover and can be spectrally confused with other benthic features such as areas of macro-algae, detritus, and corals (Mumby et al., 1997a,b). The small size and/or linear shape and patchy nature of many seagrass meadows means that in many cases high spatial resolution is also required to accurately determine their distribution and abundance. Another limiting factor in accurately detecting change in seagrass meadows may be the temporal cover of remote sensing data. The spatial extent of meadows may decline in response to human impacts or natural dynamics and may change rapidly, within weeks to months. For example, monitoring seasonal change in the extent and density of certain seagrass species would require a series of temporal cover data sets. The issue of temporal cover is being increasingly addressed with the availability of more satellite sensors, some with higher spatial resolution. The range of airborne and satellite remote sensing instruments now available offers the potential for spatial, spectral, radiometric, and temporal resolution to optimize the detection of benthic vegetation over a wide range of environmental situations. This makes remote sensing a feasible option for regular monitoring of seagrass meadows.

III. Optical Properties of the Overlying Water Column

A. Introduction

The fundamental principles of the interaction of light in water are discussed in Zimmerman and Dekker, Chapter 12 and the interaction of the light within the canopy is discussed in Zimmerman, Chapter 13. In this chapter, we further develop these principles and use them to understand how and why the remote sensing of seagrasses and associated environments is possible. An understanding of the way light interacts with the atmosphere, through the air–water interface, through the water column (and vice versa) must be obtained before it is possible to place results from scientific and applied literature, and case studies, into an overall perspective.

A remote sensing instrument measures light from the sun after it has passed through the atmosphere, interacted with the target, and has been reflected back through the atmosphere to the sensor mounted on an aircraft or a satellite. Scattering causes the light to change direction whereas absorption captures light and transforms it into another form of energy. Thus at any level within the atmosphere, and specifically just above the water surface, downwelling irradiance is composed of a direct sunlight fraction and a scattered sunlight fraction called diffuse skylight.

At the air–water interface, two processes can occur; the downwelling irradiance E_{d} is reflected due to the specular or Fresnel reflectance of the water surface, or the light is refracted (due to a density difference between air and water) and passes into the water column. For a flat water surface, the calculation of these Fresnel reflectance and refraction values is straightforward. For a rough water surface with swell, waves, and fractal wavelets, the situation becomes more complex, but it can still be calculated or may alternately be approached through observations.

The same processes affect the passage of light energy in the water column as in the atmosphere but the materials causing the scattering and absorption are different. In a natural water column above a seagrass meadow, the depth of the water itself and five water column components determine the fate of light in the water before it reaches the substratum. Pure water, colored dissolved organic matter (CDOM), phytoplankton, dead organic particulates, and mineral particulates each absorb and scatter light in a spectral (i.e. wavelength dependent) manner that is known or may be simulated. The light reaching the seagrass canopy is modified by the interaction of the downwelling irradiance with these substances and thus influences the quality of the light available for photosynthesis (see Zimmerman, Chapter 13).

B. Optical Properties of the Water Column Over a Seagrass Bed

Pure water has fixed absorption and scattering properties that are slightly dependent on temperature and salinity. CDOM is by definition dissolved and thus should not scatter light. Due to its organic composition, the color of CDOM is yellow and thus it acts as a blue light filter. Similarly, dead organic matter suspended in the water column usually has a yellow to brown color and also acts as a blue light absorber. The photosynthetic light harvesting pigments of phytoplankton absorb strongly in characteristic wavelengths. The most important pigment is chlorophyll a, which has in vivo absorption maxima at 438 and at 676 nm although many accessory photosynthetic and photoprotective pigments contribute to absorption over a range of visible wavelengths. The cell components and cell walls of phytoplankton also scatter light, particularly if cells contain large gas vacuoles. Mineral matter (clays and silts) absorbs light depending on the color of the source material. This color can vary from white to gray, black in extreme cases, or it may have various hues of yellow, brown, or red. All particulate matter (algae, dead organic matter, and mineral matter) scatters light; the amount and spectral shape of scattering is determined by the particle size distribution and the refractive index of the particles.

Fig. 2 shows absorption and scattering spectra of the various components in the water column from a coastal water site in Australia. The asterisks superscript denote a specific absorption or scattering; i.e. where the true spectral absorption or scattering has

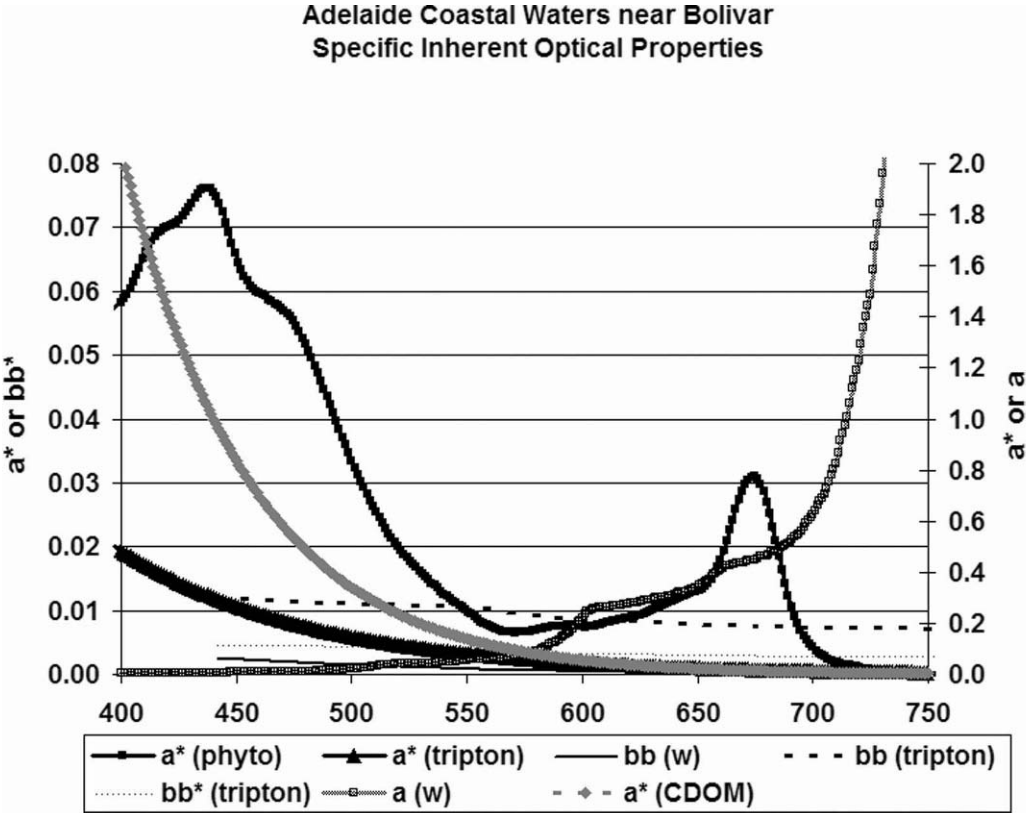

Fig. 2. Specific inherent optical properties of Bolivar test site near Adelaide (Australia). (A) Absorptions. Left axis: a^*(ph) (specific absorption by phytoplankton) and a^*(tr) (specific absorption by tripton); right axis: a(w) (absorption by water), and $a^*(\mathrm{CDOM})_{\mathrm{norm}\,440}$ (absorption by dissolved organic matter normalized at 440 nm); (B) Backscattering: b_b(w) (backscattering by water), b_b^*(ph) (specific backscattering by phytoplankton), b_b^*(tr) (specific backscattering by tripton). Units: a and b_b in (m^{-1}); a^* and b_b^* of phytoplankton in (mg m^{-2} and a^*(tr) and b_b^*(tr) in (g m^{-2}).

been divided by the concentration of the absorbing or scattering substance. Chapter 13 explains how absorption and scattering of light occur in the seagrass canopy.

Turbidity is a poor descriptor of the underwater light field since it may result from any combination of the above-mentioned optical properties. Take for example an extreme case of water with very high concentrations of CDOM but no particulate scattering matter. Could this be considered as turbid water? In this case, the water would increasingly absorb light from the yellow, through the green to a maximum in the blue wavelengths. The broad blue spectral band in which the chlorophylls and carotenoids of seagrasses and other aquatic plants absorb maximally would receive no light after a few tens of centimeters. Thus, in the blue this water is opaque and a signal at these wavelengths will not be detected by remote sensing, whereas in the orange and red wavelengths most light would still penetrate to the substratum to a depth of a few meters. The water would appear as a clear yellow to orange color. Water containing a high concentration of suspended sediments may, on the other hand, be relatively opaque across all the visible wavelengths while very clear water shows minimal absorption in the blue with absorption increasing towards the red wavelengths.

For this reason, spectral light availability at different depths should be discussed in terms of the wavelength dependent attenuation of light due to absorption and scattering processes. These properties are usually measured in a water column using a downwelling irradiance sensor (i.e. with the sensor pointed upwards) to measure the parameter, K_d. The attenuation of light going from the surface down into the water column, K_u, is measured using an upwelling irradiance sensor (i.e. with the sensor pointed downwards). Attenuation of the light that has either reached the substratum and is reflected from it, or the light that is scattered upward in the water column and travels upward, is defined as the attenuation with decreasing depth (κ). Unfortunately, κ cannot be measured directly but must be estimated through RT modeling. These important variables of the underwater light field determine the fate of light that passes into, and out, of the water column after interacting with the water column and the substratum (cf. Chapter 13). The resultant light traveling in an upward direction may ultimately be detected and measured by a remote sensor.

IV. Optically Deep and Shallow Waters: Physical Definitions

Chapter 12 presented an introduction to the fundamental principles of the interaction of light in water. A more detailed explanation is essential for understanding the signal measured by remote sensing over a seagrass area. Here, we expand these concepts making use of all the quantities and variables defined in Chapter 12. Dekker et al. (2001) have presented a comprehensive review of the remote sensing of aquatic ecosystems: the following discussion, on the analytical model of the underwater light field, is based on that review.

A. Optically Deep Waters

In order to understand the relationship between the subsurface irradiance reflectance over a water body and related substratum visibility it is necessary to first understand the subsurface irradiance reflectance of a water body where only the water column is visible, i.e. in optically deep waters. Very clear natural waters may be 30, 40 or more than 50 m deep before the water can be considered optically deep. In waters with very high concentrations of absorbing and scattering substances such an ‘optically deep’ water body may occur when the benthic vegetation or substratum is only submerged under half a meter of water. Thus, benthic vegetation may be detectable to depths of tens of meters in the clearest waters but only to tens of centimeters in high light absorbing and scattering waters.

We refer to Aas (1987) for a complete derivation of the analytical model for the irradiance reflectance over an optically deep water body. The reason for choosing this model is that it acts as a reference for understanding all other models of this kind found in the literature (Dekker et al., 2001). In terms of the backscattering and absorption coefficients, the Aas (1987) analytical model for irradiance reflectance can be written as

$$R(0-) = \frac{r_{\mathrm{d}}\bar{\mu}_{\mathrm{u}}}{\bar{\mu}_{\mathrm{u}} + \bar{\mu}_{\mathrm{d}}} \frac{b_{\mathrm{b}}}{a + kb_{\mathrm{b}}},$$
$$k = \frac{r_{\mathrm{d}}\bar{\mu}_{\mathrm{u}} + r_{\mathrm{u}}\bar{\mu}_{\mathrm{d}}}{\bar{\mu}_{\mathrm{u}} + \bar{\mu}_{\mathrm{d}}} \tag{1}$$

To specify the model in Eq. (1), four parameters are required, namely $\bar{\mu}_{\mathrm{d}}$, $\bar{\mu}_{\mathrm{u}}$, r_{d}, and r_{u}, where r_{u} and r_{d} are the shape factors for up and downward scattering, respectively (the average cosines for downwelling and upwelling light $\bar{\mu}_{\mathrm{d}}$, $\bar{\mu}_{\mathrm{u}}$ are explained in Chapter 12). The shape factors describe the difference between the backward and upward scattered fraction of light and the forward and downward fractions of light. For vertically incident irradiance these are unity. Despite the approximations applied in this model (Aas, 1987), it may be expected to yield quite accurate results for turbid waters.

B. Optically Shallow Waters

The discussion of the analytical model for optically shallow waters was based mainly on Maritorena et al. (1994), slightly adapted and reformulated to ensure consistency in terminology and definitions. Maritorena et al. (1994) present a clear discussion of the physics of an optically shallow water body where part of the reflectance at the surface is composed of a bottom signal, using an approach derived from the two-flow equations. The following text is mainly derived from their text; however, the notation has been adapted for consistency.

In optically shallow waters, $E_{\mathrm{u}}(0-)$ can be defined as the sum of $E_{\mathrm{u}}(0-)_{\mathrm{C}}$, the upwelling irradiance originating from within the water column (where none of the photons have interacted with the substratum), and $E_{\mathrm{u}}(0-)_{\mathrm{B}}$, the upwelling irradiance reflected from the substratum (where each of the photons have interacted with the substratum):

$$E_{\mathrm{u}}(0-) = E_{\mathrm{u}}(0-)_{\mathrm{C}} + E_{\mathrm{u}}(0-)_{\mathrm{B}} \tag{2}$$

To estimate the first term of the right hand side consider an infinitely thin layer of thickness dZ at depth Z, where the downwelling irradiance is $E_{\mathrm{d}}(Z)$.

At this depth, the fraction of upwelling irradiance 'created' by this layer is

$$-\mathrm{d}E_\mathrm{u}(Z) = b_\mathrm{ud}E_\mathrm{d}(Z)\mathrm{d}Z \tag{3}$$

where b_ud is the diffuse attenuation coefficient for upward scattered light. Before it reaches the surface, $\mathrm{d}E_\mathrm{u}(Z)$ is attenuated along the path from Z to the surface, according to $\exp(-\kappa Z)$, where κ is the vertical diffuse attenuation coefficient for $E_\mathrm{u}(Z)$ as defined by Kirk (1989). Note that K_u represents the vertical attenuation coefficient for diffuse upwelling light, E_u, measured from the surface downwards, whereas κ is the vertical attenuation coefficient for diffuse upwelling light originating in each layer of the water column and measured upwards from lower depths. The contribution of the considered layer in Eq. (3) to the upwelling irradiance just below the water surface is expressed as

$$-\mathrm{d}E_\mathrm{u}(Z \to 0) = b_\mathrm{ud}E_\mathrm{d}(0-) \times \exp[-(K_\mathrm{d}+\kappa)Z]\mathrm{d}Z \tag{4}$$

If it is assumed that b_ud, K_d, and κ are not depth-dependent, then the contribution of all layers between Z and 0 is

$$E_\mathrm{d}(0-, Z) = b_\mathrm{ud}E_\mathrm{d}(0-)\int_0^Z \times\exp[-(K_\mathrm{d}+\kappa)Z]\mathrm{d}Z \tag{5}$$

Equivalent to:

$$E_\mathrm{u}(0-, Z) = (K_\mathrm{d}+\kappa)^{-1}b_\mathrm{ud}E_\mathrm{d}(0-) \times(1-\exp[-(K_\mathrm{d}+\kappa)Z]) \tag{6}$$

For an infinite water depth Eq. (6) reduces to:

$$\begin{aligned} E_\mathrm{u}(0-, \infty) &= (K_\mathrm{d}+\kappa)^{-1}b_\mathrm{ud}\,E_\mathrm{d}(0-) \\ &= R_\infty E_\mathrm{d}(0-) \end{aligned} \tag{7}$$

where R_∞ represents the subsurface irradiance reflectance $R(0-)$, as given in Eq. (1), of an hypothetical optically deep water column. If we assume a totally absorbing substratum at depth H, Eq. (6) becomes

$$\begin{aligned} E_\mathrm{u}(0-, H) &= R_\infty E_\mathrm{d}(0-)(1-\exp[-(K_\mathrm{d}+\kappa)H]) \\ &= E_\mathrm{u}(0-)_\mathrm{C} \end{aligned} \tag{8}$$

That gives the first term in Eq. (2); the upwelling irradiance originated only from the water column. For optically shallow water with a bottom reflectance of R_b, the upwelling irradiance originating from substratum reflectance at a level H (immediately above the bottom) is

$$E_\mathrm{u}(0)_\mathrm{B} = R_\mathrm{b}E_\mathrm{d}(0)\exp[-(K_\mathrm{d}+\kappa)H]) \tag{9}$$

Because there are actually two upwelling light streams; one from the bottom and one from the water column, κ can be described as κ_B and κ_C, respectively. Substituting Eqs. (8) and (9) in Eq. (2) the following equation is obtained.

$$E_\mathrm{u}(0-) = E_\mathrm{d}(0-)(R_\infty + \exp(-K_\mathrm{d}H) \times [R_\mathrm{b}\exp(-\kappa_\mathrm{B}H) - R_\infty\exp(-\kappa_\mathrm{C}H)] \tag{10}$$

When we divide Eq. (10) with $E_\mathrm{d}(0-)$ we arrive at the expression for the reflectance just below the surface of a homogeneous water body with a reflecting substratum:

$$R(0, H) = R_\infty + \exp(-\kappa_\mathrm{d}H)[R_\mathrm{b}\exp(-\kappa_\mathrm{B}H) - R_\infty\exp(-\kappa_\mathrm{C}H)] \tag{11}$$

This equation reads as: The subsurface irradiance reflectance measured over a water body with bottom visibility is equal to the subsurface irradiance reflectance of an infinitely deep water column plus the product of the vertical downward attenuation of the downwelling light stream times the difference between the vertical upward attenuated bottom irradiance reflectance and the vertically upward attenuated infinitely deep water column irradiance reflectance. If one is not able to separate the two upwelling light streams, assuming that $\kappa_\mathrm{B} = \kappa_\mathrm{C} = \kappa$, then Eq. (11) simplifies to:

$$R(0-, H) = R_\infty + (R_\mathrm{b} - R_\infty) \times \exp[-(K_\mathrm{d}+\kappa)H] \tag{12}$$

which is identical to the formulation of Philpot (1989). Furthermore, if it is impossible to estimate the vertical diffuse attenuation coefficient κ of upwelling light, assuming $\kappa = K_\mathrm{d}$, Eq. (12) simplifies further to:

$$R(0-, H) = R_\infty + (R_b - R_\infty) \times \exp[-2K_d H] \quad (13)$$

which is identical to the formulation of Bierwirth et al. (1993).

The above formulations form the basis for remote sensing of a substratum covered by a water column. As Chapter 13 illustrates, though, the complexity of the seagrass canopy geometry due to leaf form and movement with waves and currents, is not incorporated into these analytical derivations. A merger between these two analytical models (for water column and seagrass canopy) is required for improved understanding of the effects of seagrass canopy structure and variability of the remotely sensed signal.

V. Methodological Approaches to Assessing Seagrass Ecosystem Characteristics from Remote Sensing

What are the consequences of these formulations for the remote sensing of seagrasses? Before we answer this question, we need to discuss possible approaches to remote sensing of seagrasses from the simple to the more complex.

A. Choice of Methods

1. The Empirical Method

This is the favorite methodology for seagrass mapping and uses whatever remote sensing imagery may be readily available at the study site using traditional supervised or unsupervised classification procedures together with fieldwork to identify the characteristic substratum types that appear in the image including benthic plant species and other cover classes. Fieldwork is preferably carried out during the overpass of the remote sensor, but in practice fieldwork is often performed days to weeks before or after collection of the imagery. As the remote sensing image usually covers a much larger area than surveyed during fieldwork, extrapolation is performed using a variety of either subjective (worst case) or statistically developed (best case) techniques. No explicit use is made of spectral bands or their positioning. Unfortunately there is no guarantee that the extrapolations are valid, nor can this methodology deal with atmosphere, air–water interface, or water column depth differences or with substratums and vegetation covers that were not present in the fieldwork. Another significant drawback is that it is impossible to detect multitemporal change in an objective manner, nor is it possible to transfer the image classes developed using this technique to other areas or other images without having to repeat all the fieldwork and analysis. Thus, this method relies heavily on local expert knowledge.

2. The Semi-empirical or Semi-analytical Method

With this approach, the results gained from using a traditional classification procedure are improved by applying some a priori knowledge of the spectral behavior of the substratum and vegetation cover classes in consideration of the spectral bands available from the remote sensing instrument before image acquisition. An optimal band set is selected for a specific mapping purpose. In the case of hyperspectral sensors or sensors with programmable bands, the entire range of useful spectral bands may be collected. Joyce and Phinn (2003) were able to assess chlorophyll content and photosynthetic capacity of coral reef substratum using hyperspectral measurements using a spectral matching approach. Andrefouet et al. (2003) were able to discriminate chlorophylls, carotenoids, and phycobilin pigments over microbial mats on a coral atoll using airborne imaging spectrometry data and by applying derivative analysis. Both the studies indicate that this will become possible for seagrasses too.

3. The Analytical Method

With this method, the radiative transfer equations can be simplified for the retrieval of the variables of interest, and hence, the weak benthic signal containing the desired layer of information about the seagrasses can be untangled from remote sensing image data. For instance, Eq. (11) (or the more detailed equations preceding that derivation) can be inverted for a spectral band to enable the determination of one variable such as bottom reflectance (R_b) provided that all the other variables are known or can be estimated. When based solely on the remote sensing reflectance, only ($R(0-,H)$) is measured (after atmospheric and air–water interface correction).

As more spectral bands become available it becomes possible to determine more variables. In theory, if we have two spectral bands (containing some uncorrelated information) then two variables can be directly retrieved, with three spectral bands three variables can be directly retrieved, and so on. These variables do need to have a measurable influence (from an aircraft or space sensor) on the spectral band reflectances!

To obtain bottom reflectance (R_b), we would need to invert Eq. (11) and to do this we would need to be able to determine two reflectances ($R(0-, H)$ and R_∞), four vertical attenuation coefficients (K_d, K_u, κ_B, and κ_C) and the water column depth, which would require a minimum of eight spectral bands for direct inversion calculations. Since the vertical attenuation coefficients are spectrally similar and potentially spatially variable (e.g. Karpouzli et al., 2003), it is difficult to determine these directly from remotely sensed image bands.

A solution to this problem is to look at the inherent optical properties of absorption, scattering, or preferably backscattering of each of the components of the water. The spectral shapes of these components are more specific and thus have a better chance of being estimated from spectral information. The vertical attenuation coefficients can then be calculated from the inherent optical properties. Inversion of an 8 band, 8 variable set of equations (that contain some nonlinear effects) is virtually impossible, especially if one realizes that all the remote sensing data contain some level of noise. Solutions are possible; but these will be discussed only after considering another pathway to understanding the underwater light climate and the detection of substratum reflectance: the Radiative Transfer of Energy theory (RT) based modeling approach (see Chapter 12 for introduction to RT theory and Chapter 13 for the application of RT theory to seagrass canopy light interactions).

4. Numerical Modeling of the Underwater Light Field

The fundamental principles of all optical processes are incorporated within Radiative Transfer of Energy theory (RT). RT explains how the radiometric properties, i.e. the radiance and irradiance, change in the water column due to the optical properties of the medium. Mobley (1994) and the software package Hydrolight based on that book are the current state-of-the-art tools for exact modeling of the underwater light field. The Hydrolight model does require accurate input on sun position and atmospheric conditions (including wind speed at the surface), inherent optical properties of each of the optical components and substratum or benthic vegetation reflectance. Once these are available, it will calculate all apparent optical properties such as attenuation coefficients, reflectances from just above the substratum to those above the air–water interface, and so on. The average cosines and diffuse inherent optical properties can also be calculated. Since the user may define many layers of water with differing optical properties, all conceivable permutations of water columns can be calculated.

Unfortunately, it is not possible to directly invert an RT model to derive the variables of interest because the calculations involve tracing the fates of fluxes of photons through few to many interactions with the pure water, its constituents and the substratum and its vegetation cover.

B. Analytical and/or Radiative Transfer-Based Inversion Schemes for Remote Sensing of Seagrasses

Two main pathways are therefore available for inverting a remote sensing image to produce a benthic map, e.g. a map of seagrass distribution or some other benthic map.

One approach is to use the analytical model for inversion, whereby the forward analytical model is parameterized by, amongst others, the RT simulations. The analytical inversion methods are fast and traceable, although the results will always be based on the necessary simplifications inherent in analytical equations.

The other approach is to use inversion methods such as matching remotely measured spectra with lookup tables or neural network inversions, requiring significant computing time either in their preparation or in applying them to a remote sensing image. Increased computing power will make this task easier in the future. Louchard et al. (2003) applied the lookup table approach using matching spectra to airborne imaging spectrometry data over Lee Stocking Island in the Bahamas and were able to determine water column depth as well as three sediment classes, five cover classes of *Thalassia testudinum* (in steps of 20%) and coral cover and coral rubble. Dierssen et al. (2003) using the same hyperspectral airborne data over Lee Stocking Island were able to determine water column depth and leaf area index of *Thalassia testudinum*. Kutser et al. (2003) used Hydrolight RT-modeling to assess the airborne and spaceborne hyperspectral data discrimination of substratum and substratum cover over coral reefs. They could discriminate eight substratum types of coral, algae, and cyanobacteria.

Analytical- and RT-based forward and inverse models have several strong advantages over any of the other methods applied, presuming that a remote sensing image has already been corrected for atmospheric and air–water interface effects.

1. Repeatability—multitemporal images can be compared quantitatively as the methodology is objective and physics-rules based. Corrections for changing water column depth (tides!) and varying concentrations of water column constituents is possible.
2. Transferability—application of the models to data from other sensors is straightforward and only involves adaptation of the spectral bands.
3. Sensitivity and error analysis are exact and objectively determined. Once initialized, processing of images is fast compared to human interpreter based methods (seconds, minutes, or at the most hours for a remote sensor image).
4. New knowledge can be added to the simulations, and can be retrospectively applied to remote sensing images.
5. Archival remote sensing data (e.g. Landsat TM data from 1984 onwards) can be processed according to the currently developed methodology. The fact that no field measurements are available from the past does not prevent analysis of the images; the only assumption is that the more recent spectral information is correct in shape for each of the components as illustrated in the Landsat-based seagrass change detection study by Anstee et al. (2004).

VI. Conclusions, Recommendations, and Outlook

Future developments (see also Malthus and Mumby, 2003) in the areas of airborne and spaceborne sensors, underwater optical instrumentation, spectral libraries, improved bathymetric datasets, simulation and inversion methods, and the integration of remote sensing with other methodologies will lead to accelerated development of methods for the remote sensing, mapping, and monitoring of seagrass meadows. Remote sensing offers one of the most versatile and accurate techniques for seagrass assessments at any scale (down to ground resolutions of 0.5 m), where field methods cannot be used to accomplish the required task in a reasonable time. There is a trend for remotely sensed data to become more cost-effective, either because of the real reductions in the cost of raw data for multispectral imagery, or because of the increase in the number of indicators that can be retrieved using airborne hyperspectral data.

The sophisticated procedures applied to derive benthic maps from digital multispectral or hyperspectral remote sensing require a combination of mathematical, software, hardware, physics, and biogeochemistry skills that currently restrict management institutions from investing in this data acquisition capability. In contrast, seagrass maps can be routinely produced by seagrass experts within an organization using aerial photographs. Despite high spatial resolution, the poor spectral resolution of aerial photography is insensitive to subtle spectral variations and limits the successful discrimination of submerged features (e.g. Holden and LeDrew, 1999). It would require only minimal training in the use of remote sensing software for these same staff to produce more accurate seagrass maps of higher information content using the simpler empirical and semi-empirical methods for image analysis. Though it may require higher investment to procure the higher quality seagrass products based on analytical or RT modeling at present, the cost should be balanced against the type, quantity, and accuracy of information such techniques can provide. It is likely that remote sensing from aircraft and satellites will be the methods more often applied in the future. Indeed in the coral reef community, worldwide spectral library measurement programs (13,000 spectra collected; see Hochberg et al. (2003)) have led to a demand for remote sensing of coral reef ecosystems. The seagrass community should also carry out a worldwide spectral library collection program (including the measurement of co-occurring benthic micro-algae, macro-algae, sediment, and rock substratum), to mature the field of hyperspectral remote sensing (by standardizing processing methods) for use by seagrass biologists in their studies.

Merging the seagrass canopy structure geometry analysis by Zimmerman in Chapter 13 into the underwater RT or analytical optical models required for quantitative remote sensing, will further advance our understanding of the remotely sensed signal over a water body with seagrass cover. As the spectral response of seagrasses to environmental pressures is better understood, sophisticated remote sensing of this spectral response may open up many more applications in seagrass biology. Spatially comprehensive maps of changes in seagrass species or epiphytic algae abundance, will lead to new insights into cause and effect of seagrass ecosystem change, not possible by aerial photography analysis.

The insight into the relationship between light and photosynthesis (Zimmerman, Chapter 13) and the insight into advanced remote sensing based methods for estimating water column and substratum vegetation cover both point to a future convergence where photosynthetic studies in seagrass meadows will use information derived from remote sensing and vice versa.

A challenge will be to merge all the historical information provided by aerial photograph interpretation and field knowledge gathered on seagrass meadows in the last century with these spectral measurement and analysis methodologies (be it remote sensing or field-based), in order to create improved knowledge on seagrass extent and distribution, leading to improved understanding, and management practices. Another challenge is to provide accurate estimation of a sloping seabed; for instance *P. australis* beds, which, in the Australian Bight, may go down to >30 m, sometimes below the optical depth of the water column.

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Chapter 16

Zostera: Biology, Ecology, and Management

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I. Introduction

The nine species comprising the genus *Zostera* discussed in this chapter form a widespread and relatively well-studied group of seagrasses. Some of the earliest studies of seagrasses occurred within the genus *Zostera*, especially the extensively researched *Zostera marina* L. (Petersen, 1890, 1918). The proximity of this species to industrialized areas and centers of scientific investigation in North America, Europe, and Asia has encouraged a continued scientific focus. Like all seagrasses, those of the genus *Zostera* live in intertidal and subtidal inshore waters, forming a critical habitat and a basis of the food web. Study of the genus *Zostera* is itself representative of trends in seagrass science, with PAM fluorometry assessments of photosynthesis and genetic investigations among the newer efforts. We here review the current knowledge of this important genus, although space constraints do not allow exhaustive coverage of all past and current *Zostera* research. We also point to future research directions.

II. Comparative Biology

A. Taxonomic Overview

All *Zostera* species are in the family Zosteraceae. The genus is characterized by species that are monoecious with monopodial, creeping rhizomes that are usually perennial (den Hartog, 1970; Tomlinson, 1982; den Hartog and Kuo, Chapter 1). *Zostera* shoots are characterized by both vegetative foliage leaves and sexually reproductive stems with spike-like spadices and unisexual flowers on one flattened side. Most are mono-meristematic leaf-replacing species (Short and Duarte, 2001), although *Zostera japonica* is a di-meristematic leaf-replacing species and the erect shoots of *Zostera tasmanica* can become secondarily rooted and form new rhizomes. There are ongoing discussions about the taxonomy of the family Zosteraceae, the genus *Zostera*, and species designations within the *Zostera* genus (Kuo, 2001; Kuo and den Hartog, 2001; Tomlinson and Posluzny, 2001; Les et al., 2002). Species recognition in *Zostera* in some regions has been difficult due to wide intra-specific variability that makes the use of taxonomic characters subjective (Green and Short, 2003). Ultimately, accurate taxonomic speciation will require a combination of approaches including molecular evidence and morphological analyses (Tomlinson and Posluzny, 2001). The species designations of the *Zostera* species of Australia and New Zealand, in particular, have recently been revised (Les et al., 2002) with merger of the Australian/New Zealand *Zostera* within the single species *Zostera capricorni* and renaming of the genus *Heterozostera* to *Zostera*. *Zostera novazelandica* Setchell and *Z. capricorni* Ascherson, found throughout the coasts of New Zealand, from Parengarenga Harbour in the north to Stewart Island in the south (Inglis, 2003), were found to be conspecific. The Australian species,

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Fig. 1. Zostera tasmanica (formerly *Heterozostera tasmanica)* in a surge zone off Perth, Australia. Photo: F. Short.

Zostera muelleri Irmisch ex. Aschers. and *Zostera mucronata* den Hartog were also found to be conspecific with *Z. capricorni* (Les et al., 2002; Spalding et al., 2003). *Zostera tasmanica*, formerly *Heterozostera tasmanica* (Fig. 1), was determined to be a distinct *Zostera* species found in southern Australia and in Chile. These changes have not been accepted by all taxonomists at the present time and the reader is referred to den Hartog and Kuo, Chapter 1, for the previous taxonomy based on morphological and ecological characteristics.

For the purposes of this review the genus *Zostera* is composed of the following species:

Zostera asiatica Miki
Zostera caespitosa Miki
Zostera capensis Setchell
Zostera capricorni Ascherson (including the former *Zostera mucronata*, *Zostera muelleri*, and *Zostera novazelandica*)
Zostera caulescens Miki
Zostera japonica Aschers. & Graebner (formerly *Zostera nana* in the northwest Pacific and *Zostera americana* in the northeast Pacific)
Zostera marina Linnaeus
Zostera noltii Hornemann
Zostera tasmanica Martens ex Ascherson (formerly *Heterozostera*).

B. Geographical Distribution

The world maps of *Zostera* species (Green and Short, 2003) demonstrate the success of this genus through its broad distribution in most of the world's oceans

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Abbreviations: PAM – pulse amplitude modulated (fluorometer); psu – practical salinity unit (≡ part per thousand) (see http://oceanworld.tamu.edu/resources/ocng_textbook/chapter06/chapter06_01.htm)

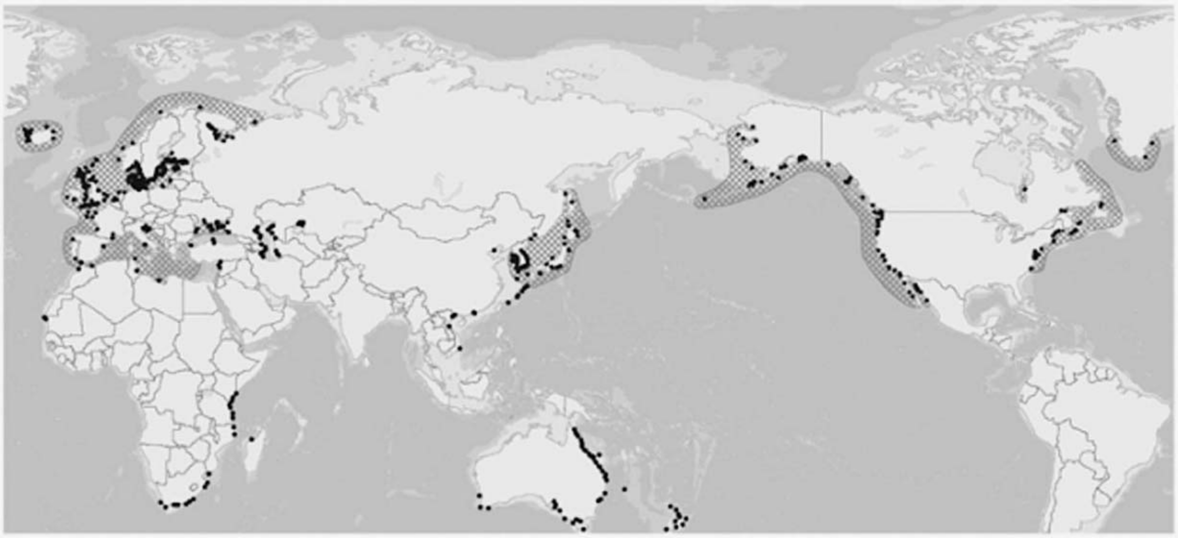

Fig. 2. Worldwide distribution of all *Zostera* species (dots indicate literature reports); shaded area indicates the range of *Zostera marina* (Green and Short, 2003).

as well as the Black, Caspian and Aral Seas (Fig. 2). *Zostera* species are found over the largest latitudinal range of any seagrass genera, ranging from the tropics to the Arctic and sub-Antarctic. In the tropics of the western Pacific and Indian Ocean, *Z. japonica* is reported as far south in the northern hemisphere as Viet Nam (Huong et al., 2003) and *Z. capensis* occurs in the southern hemisphere from South Africa to as far north as Kenya (Ochieng and Erftemeijer, 2003). The most northerly locations reported for seagrasses are for *Z. marina* at Veranger fjord in Norway (70°30′N), Chëshskaya Guba in Russia (67°30′N) and in Alaska (at 66°33′N) (Green and Short, 2003). The most southerly seagrass locations are *Z. capricorni* in New Zealand, with the southernmost population reported at 46°55′S on Stewart Island (Green and Short, 2003).

Z. marina is the dominant seagrass found in coastal and estuarine areas of the western North Atlantic (Short and Short, 2003), a region considered here as the Atlantic coast from Quebec (Canada) at approximately 60°N to North Carolina (United States) at 35°N. *Z. marina* is found in Hudson Bay, Newfoundland and Nova Scotia, though absent from the northern coastline of the Bay of Fundy. In the northern US, *Z. marina* forms extensive beds that occupy the full range of *Z. marina* habitat conditions, from the high intertidal to the subtidal, and from sheltered areas to exposed coasts (Fig. 3). In central New England, *Z. marina* grows from a depth of +2 m to −12 m mean sea level (MSL) (Short et al., 1993a). *Z. marina* occurs predominantly in a mono-culture throughout most of its distribution, although it sometimes co-occurs with a variety of species: in the US, mid-Atlantic it co-occurs with *Ruppia maritima* or *Halodule wrightii* which can dominate intertidal and shallow subtidal areas (Orth and Moore, 1983b; Ferguson et al., 1993); in the eastern North Atlantic and Mediterranean, *Z. marina* co-occurs with *Z. noltii,* which similarly dominates in intertidal and shallow subtidal areas (Marba et al., 1996; Harrison, 1999); in the eastern Pacific, *Z. marina* occurs from the Baja Peninsula and the Sea of Cortez in Mexico north to Alaska where it overlaps the distributions of *R. maritima, Z. asiatica, Z. japonica,* and three *Phyllospadix* species (Wyllie-Echeverria and Ackerman, 2003); in the northwestern US and Canada, *Z. marina* grows in the lower intertidal and subtidal, where it co-occurs with *Z. japonica*, which is found growing higher in the intertidal (Bulthuis, 1995). For example in British Columbia, Canada, Baldwin, and Lovvorn (1994a,b) reported *Z. japonica* occurring from 0 to −1.8 m MSL with *Z. marina* occurring from −0.9 to −5.5 m MSL; in northern Europe, *Z. marina* was historically found in abundance from the coast of Spain throughout the North and Baltic Seas to the White Sea in Russia, and often co-occurred with *Z. noltii* (see below); however, much of the early distribution has been lost, particularly in The Netherlands, England, and the Baltic Sea (see Kenworthy et al., Chapter 25)

Fig. 3. Expansive intertidal *Zostera marina* meadow in Maquoit Bay, Maine, USA. Photo: F. Short.

Z. noltii occurs along the coasts of Europe and northern Africa, growing in the intertidal region, often with *Z. marina* which extends to greater depths (Green and Short, 2003). *Z. noltii* is reported in the Baltic Sea, the Wadden Sea, United Kingdom, Ireland, Gulf of Moribihan, and Arachon Basin where it forms extensive beds on tidal flats (Marbà et al., 1996; Harrison, 1999; Boström et al., 2003; Hily et al., 2003). In the Mediterranean, it co-occurs with *Cymodocea nodosa* as well as *Z. marina* and is found from intertidal flats to subtidal depths of 1–2 m (Lipkin et al., 2003; Procaccini et al., 2003). Additionally, its distribution ranges to the Black, Azov, Caspian, and Aral Seas where it has persisted in shallow bays and coves but has also been reported growing to depths of up to 10 m (Milchakova, 2003).

Z. japonica is a small seagrass inhabiting intertidal and shallow subtidal bottoms along the Pacific coast of Asia from Viet Nam to northern Russia (Lee, 1997; Shin and Choi, 1998). In Japan, *Z. japonica* is found from the northeastern part of Hokkaido to the Sea of Japan (Aioi and Nakaoka, 2003). On the Pacific coast of North America, *Z. japonica* is an invasive species extending from British Colombia, Canada to Oregon, USA, believed to be introduced with oyster culture from Japan (Harrison and Bigley, 1982; Posey, 1988).

Z. capricorni is the dominant *Zostera* species found along the east coast of Australia, where it predominates in inshore areas (Conacher et al., 1994). In South Australia, *Z. capricorni* distribution overlaps that of *Z. tasmanica* (formerly *Heterozostera tasmanica*). *Z. capricorni* (formerly *Z. mucronata)* was also reported from both south and south-western Australia, where it occurs with *Halophila ovalis* and *Halophila decipiens* (Kuo and Kirkman, 1995) as well as *Z. tasmanica* and *Z. capricorni* (formerly *Z. muelleri*).

Z. capensis is the only *Zostera* species in the Indian Ocean and is restricted to the south and east coasts of Africa (Talbot and Bate, 1987; Green and

Table 1. Morphological comparison of the *Zostera* genera, modified from Kuo and den Hartog (2001) and Phillips and Meñez (1988).

Species	Typical length (cm)	Width (mm)	Leaf tip	Seed length (mm)
Zostera asiatica	100	7.0–15.0	Flattened notched	3.0–5.0
Zostera caespitosa	50	2.5–4.5	Rounded slightly notched	3.0–3.5
Zostera capensis	40	0.5–2.5	Rounded slightly notched	2.0–2.5
Zostera capricorni	30	0.5–5.0	Slightly rounded variable	2.0–2.4
Zostera caulescens	60	10.0–13.0	Rounded with point	3.5–4.5
Zostera japonica	20	0.8–1.2	Rounded slightly notched	2.0
Zostera marina	80	3.0–12.0	Rounded	3.0–4.0
Zostera noltii	20	0.5–1.5	Rounded often notched	1.5–2.0
Zostera tasmanica	30	0.5–3.0	Pointed/rounded notched	2.0–4.0

Short, 2003). *Z. capensis* is the most widespread and one of the dominant seagrass species in South Africa (Bandeira and Gell, 2003) and is found associated with a variety of other species including *Cymodocea serrulata, Cymodocea rotundata, Halodule wrightii, Halodule uninervis, Thalassodondron cilatum, Thalassia hemprichii, Halophila ovalis,* and *Syringodium isoetifolium* (de Boer, 2000; Paula et al., 2001; Bandeira, 2002). *Z. capensis* occurs mostly in estuarine waters from Kwazulu-Natal to the western Cape region (Bandeira, 2002; Bandeira and Gell, 2003).

In the Asian northwestern Pacific, up to five species of *Zostera* have been reported: *Z. japonica, Z. marina, Z. asiatica, Z. caulescens, Z. caespitosa* (Shin and Choi, 1998). Lee et al. (2000) reported that on the eastern coast of Korea, the depth of *Z. asiatica* (-8.5 to -15.0 m) exceeded that of *Z. marina* (-1.3 to -5.6 m) and *Z. caespitosa* (-3.2 to -5.2 m). Similarly in California, *Z. asiatica* is reported to depths of -5 to -17 m mean low water (Phillips and Wyllie-Echeverria, 1990). *Z. asiatica* is a cold-water, deep-growing seagrass extending from the eastern coast of the Korean Peninsula to southern Sakhalin, Russia (Miki, 1993). In Japan, it is currently known only in Hamanaka and Akkeshi Bay, Hokkaido, and in Funakoshi Bay, on the northeastern coast of Honshu (Aioi and Nakaoka, 2003). *Z. asiatica* has also been reported at three sites on the Pacific coast of California (Phillips and Wyllie-Echeverria, 1990). *Z. caulescens*, a very large seagrass, is reported from limited localities along the central to northern coast of Honshu in northeastern Japan (Aioi et al., 1998) and the southern coast of the Korean Peninsula (Shin and Choi, 1998). In Funakoshi Bay, Japan (36°26′N and 141°04′E) flowering shoots of over 7 m have been collected (Aioi and Nakaoka, 2003). Typical lengths of the vegetative canopy range from 3 to 4 m in water depths of >10 m. *Zostera caulescens* is the dominant species of seagrass where it occurs, with small patches of *Z. marina* and *Z. asiatica* in the shallower parts of the bed. In Korea, *Z. caulescens* is also reported to have exceptionally long flowering shoots, reaching 8 m (Lee and Lee, 2003). *Zostera caespitosa* is found in Hokkaido and in the northern half of Honshu in Japan (Taniguchi and Yamada, 1979; Nakaoka and Aioi, 2001), and on the Korean Peninsula (Shin and Choi, 1998).

C. Morphology

The morphology of *Zostera* species varies widely, from the relatively small and narrow-leaved intertidal species such as *Z. japonica* and *Z. noltii* to species with long, wide leaves such as *Z. marina* and *Z. asiatica* (Table 1). The majority of the *Zostera* species have leaf lengths from 30 to 60 cm on average, but there is a great range in leaf lengths within and among all species, depending on environmental conditions. Flowering shoots in all species of *Zostera* arise as erect, branching stems with spathes bearing both male and female flowers. The height of these reproductive shoots varies from below the canopy (as in *Z. noltii*, Kuo and den Hartog, 2001) to much longer than the canopy (as in *Z. caulescens* Aioi et al., 1998).

Morphological characteristics of *Zostera* spp. are affected by a variety of physical habitat features including substrate type (Short, 1983), depth (Lee et al., 2000), temperature (Moore et al., 1996), location (Fonseca and Bell, 1998), light and nutrient availability (Short, 1983; Abal et al., 1994; Short et al., 1995; Marbà et al., 1996), and tide and wave regimes (Fonseca et al., 1983; Koch and Beer, 1996). Many *Zostera* species demonstrate increased leaf width and length as well as increasing aboveground to belowground biomass ratios with increasing depth (Phillips and Backman, 1983; Short, 1983; Bigley and Harrison, 1986; Conacher et al., 1994; Curiel et al., 1996; Lee et al., 2000; Lerodiacounou and Laurenson, 2002). Much of this morphological change is related to differences in light availability as the plants attempt to optimize photosynthesis. In situ light manipulation experiments of many *Zostera* species (Backman and Barilotti, 1976; Dennsion and Alberte, 1982, 1986; Bulthuis, 1983; Philippart, 1995) and controlled system experiments (Harrison, 1982; Abal et al., 1994; Short et al., 1995; Moore et al., 1997) have demonstrated higher densities and productivity, but smaller shoots, under higher light conditions. Much of the influence of depth on *Zostera* plant size may also be related to different levels of sediment nitrogen and other sediment characteristics, which typically change with depth (Short, 1983; Dennison et al., 1987; Lee et al., 2000). Nutrient additions to sediment have long been observed to increase individual *Z. marina* shoot size (Orth, 1977; Dennison et al., 1987; Short et al., 1995), although this was not observed in *Z. tasmanica* (Bulthuis and Woelkerling, 1981). Physical factors such as current velocity, exposure to waves and relative water depths can have significant effects on the structure of *Zostera* meadows (Fonseca and Bell, 1998). For example, Fonseca et al. (1983) found an inverse relationship between current velocity and aboveground to belowground biomass allocation for *Z. marina* beds. High current or wave regimes may also change sediment conditions in seagrass beds by increasing the diffusive loss of pore water nutrients into the water column (Koch, 1999a; Nepf and Koch, 1999) as well as loss of organic matter (Fonseca and Bell, 1998) – see also Koch et al., Chapter 8.

D. Physiology

Investigations of seagrass physiology, covered in depth elsewhere (see Zimmerman, Chapter 13, Larkum et al., Chapter 14) have been led by studies on *Zostera*, including the early experiments on the influence of low salinity on seed germination (Arasaki, 1950) and *Z. marina*'s metabolic responses to light, temperature and salinity (Biebl and McRoy, 1971). Subsequent work has shown the response of *Zostera* to temperature, with leaf respiration increasing more rapidly than photosynthesis with rising temperature, resulting in a steady decrease in the photosynthesis-to-respiration ratio (Evans et al., 1986; Marsh et al., 1986; Bulthuis, 1987) and the occurrence of a seasonal growth optimum. For species growing in locations with temperatures above the optimum for growth, near the upper limit of thermal tolerance, an increase in annual temperature decreases productivity and distribution. *Z. marina* at the southern end of its distribution on the east coast of the US shows summer suppression as in North Carolina (Thayer et al., 1984) and Chesapeake Bay (Moore et al., 1996) where *Z. marina* flourishes during the cooler months but dies back during hot summer periods. Temperature also affects flowering (De Cock, 1981) and seed germination (Harrison, 1982; Phillips et al., 1983, Hootsmans et al., 1987).

Much evidence for the physiology of light response in seagrasses is based on studies of *Z. marina* (Dennison and Alberte, 1986; Sand-Jensen, 1989; Short et al., 1995), *Z. capricorni* (Abal and Dennison, 1996), and *Z. tasmanica* (formerly *Heterozostera tasmanica*, Bulthuis, 1983). Experimental studies have shown the effects of reduced light on photosynthesis in single *Zostera* shoots and parts of plants (Drew, 1979; Williams and McRoy, 1982; Wetzel and Penhale, 1983), documenting the photosynthesis–irradiance (P–I) curve which describes a saturating relationship of the plants to increased light. The Diving-PAM (pulse amplitude modulated fluorometer) has accelerated the investigation of in situ photosynthesis in seagrasses with studies on *Zostera* (Beer et al., 1998; Ralph and Short, 2002; Ralph et al., 2002; Campbell et al., 2003), although most Diving-PAM work has been done on other genera. For *Z. marina*, the effects of decreased light are a reduction in not only shoot morphology but shoot density, number of leaves per shoot, and growth rate (Short et al., 1993a, 1995; Moore and Wetzel, 2000). That light reduction ultimately reduces areal plant productivity has been documented for *Z. marina* (Backman and Barilotti, 1976) and for *Z. tasmanica* (Bulthuis, 1983).

The impact of salinity has been shown in the laboratory, demonstrating that low salinities stimulate germination of *Z. japonica* (formerly *Zostera nana*), *Z. marina*, *Z. noltii*, and *Z. capricorni* seeds (Arasaki, 1950; Phillips et al., 1983; Churchill et al., 1985; Hootsmans et al., 1987; Loques et al., 1990; Conacher et al., 1994), although in a field study of *Z. marina*, low sediment oxygen and decrease in temperature were found to be more important than

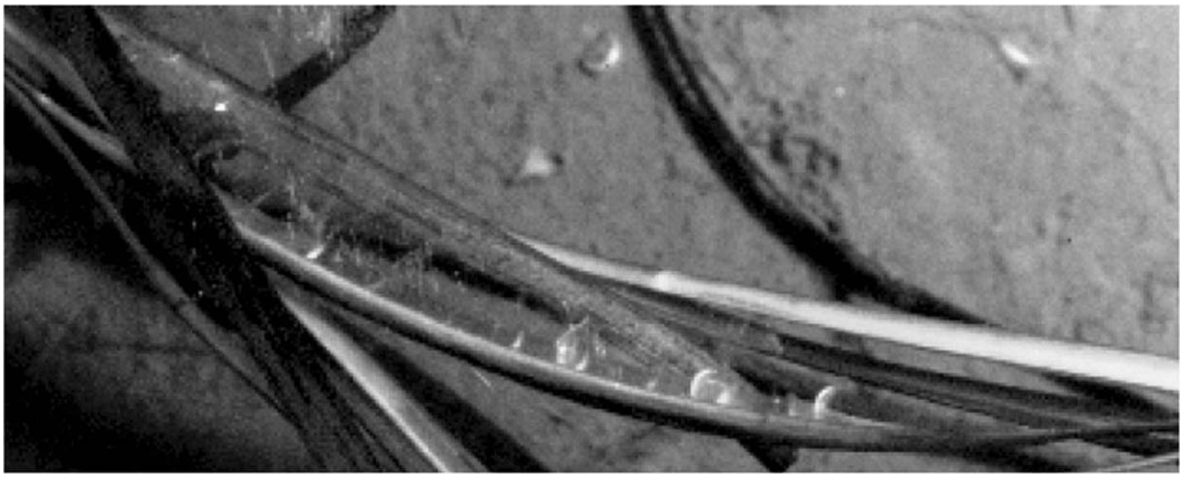

Fig. 4. Reproductive spathe of *Zostera marina* showing pollen release. Photo: F. Short.

salinity as stimulants to germination (Moore et al., 1993). Salinity produces significant osmotic stress in seagrasses. Organic acids and other plant constituents are used to counter increased osmotic pressure in *Z. marina* (van Diggelen et al., 1987) and *Z. capensis* (Adams and Bate, 1994). The vegetative propagation of *Z. capensis* in South Africa was inhibited at very high salinities as well as in fresh water (Adams and Bate, 1994). At salinity of 31 psu, *Z. marina* showed high rates of photosynthesis (Biebl and McRoy, 1971), while at both 20 and 31 psu, high rates of leaf production were found (Pinnerup, 1980). Although *Zostera* photosynthesis is maintained at low-to-intermediate salinities, productivity is reduced by up to 50% in various species at salinities less than 10–20 psu (Biebl and McRoy, 1971; Pinnerup, 1980; Kerr and Strother, 1985). Salinity is a major factor influencing the onset and severity of the eelgrass wasting disease; the pathogen *Labyrinthula zosterae* Porter et Muehlstein is stimulated at intermediate salinities ($\sim$20 psu) at which *Z. marina* starts to experience physiological stress (Muehlstein et al., 1991; Burdick et al., 1993).

Nutrient dynamics strongly influence seagrass physiology (see Romero et al., Chapter 9); some of the more detailed and extensive nutrient studies of seagrasses have been conducted on *Z. marina* (Short, 1987). Typically water column and sediment nitrogen pools limit the kinetics of nitrogen uptake through *Z. marina* leaves and roots, respectively (Iizumi and Hattori, 1982; Short and McRoy, 1984; Hemminga et al., 1994), while nitrogen acquisition limits *Z. marina* growth and productivity (Short et al., 1995). Additional studies have been conducted of nitrogen acquisition and dynamics in *Z. tasmanica* (Bulthuis and Woelkerling, 1981), *Z. capricorni* (Boon, 1986; Boon et al., 1986; Udy and Dennison, 1997), and *Z. noltii* (Kraemer and Mazzella, 1999). Under oligotrophic conditions, nutrient limitation controls plant physiology, while in eutrophic conditions nutrients cease to be limiting and nutrient stimulation of algal growth predominates (Kemp et al., 1983; Borum, 1985; Short, 1987). Recent studies suggest that excess levels of both nitrate (Burkholder et al., 1992, 1994) and ammonium (van Katwijk et al., 1997) can be toxic to *Z. marina*, although the specific toxicity levels and potential relevance under field conditions are still unclear.

E. Reproduction and Genetics

Zostera species are monoecious with flowers occurring clustered in spadices on branches along an extended stem floating vertically in the water column (Kuo and den Hartog, 2001; Walker et al., 2001). Male and female flowers occur within the same spadix (Fig. 4), with the anthers appearing first and pollen release occurring after germination in the spadix is complete. Pollen is released into the water column in linear strands which drifts within and between beds. Fruits and seeds develop within the spadix and are released directly from the parent plant or dispersed widely as spadices; alternatively, whole reproductive shoots drift under the influence of tidal currents and wind. Large numbers of seeds

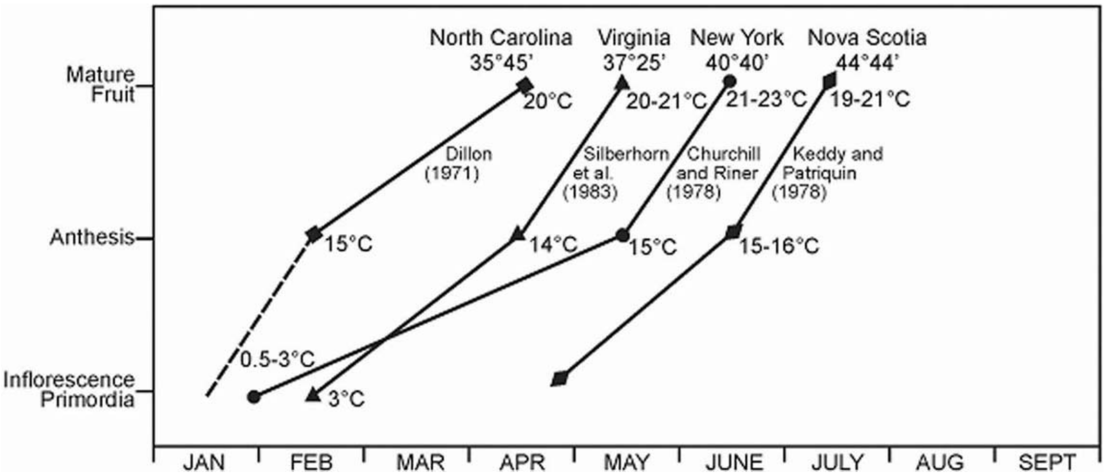

Fig. 5. Reproductive phenology of *Zostera marina* at different locations (with latitudes) along the east coast of the United States. The approximate temperature that was recorded for each event is also given (modified from Silberhorn et al., 1983).

are produced and dispersed and germination can be quite high, but only a fraction of the germinated seedlings survive to maturity.

Variations in the proportion of flowering shoots and subsequent seed production in *Zostera* populations have been well documented (e.g. Bulthuis, 1983; Orth and Moore, 1986; Strother and Kerr, 1990; Ramage and Schiel, 1998; Orth et al., Chapter 5), but many causal relationships between success of sexual reproduction and environmental factors are still not understood. Temperature is an important determinant of flowering in some *Zostera* species (De Cock, 1981), and several studies indicate that phenology of *Zostera* species is strongly related to latitude (Fig. 5), with the flowering sequence delayed as latitude increases (Phillips et al., 1983; Silberhorn et al., 1983; Walker et al., 2001). Temperature stress can be an important factor affecting sexual reproduction. The development of an annual phenotype of *Z. marina* in the Gulf of California, Mexico, has been related to high temperature (McMillan, 1983; Phillips and Backman, 1983; Meling-Lopez and Ibarra-Obando, 1999). Conversely, low temperatures and ice formation are associated with an annual form of *Z. marina* in Nova Scotia, Canada (Keddy and Patriquin, 1978; Robertson and Mann, 1984). Interestingly, the annual populations of *Z. marina* found in the Gulf of Mexico largely complete their sexual reproductive cycle before the annual high water temperatures of 30–32 °C are reached (Meling-Lopez and Ibarra-Obando, 1999), suggesting that hot summertime conditions have resulted in the selection of annual flowering strains of the species. Recent work investigating the reproductive potential of other intertidal and shallow subtidal species of *Zostera* such as *Z. noltii* and *Z. capricorni* (reported as *Z. novazelandica*) did not report strong relationships between potential stresses and reproductive output (Loques et al., 1988; Curiel et al., 1996; Ramage and Schiel, 1998). Ramage and Schiel (1998) observed that *Z. capricorni* plants growing high in the intertidal did not adopt an annual life history with a high proportion of flowering shoots. In contrast to the annual forms of *Z. marina*, maximum reproductive output of *Z. capricorni* occurred in small tide pools and low in the intertidal zone and creeks. Harrison (1993) found that intertidal populations of *Z. marina* growing in annually disturbed habitats in the southwestern Netherlands were annual. He suggested, however, that the annual life history may have been imposed on the population by a stressful environment, including grazing by geese and sediment disruption by winter storms that removed all remaining vegetative shoots. In contrast to the *Z. marina* plants, *Z. noltii* that co-occurred in the intertidal maintained a perennial population with no seed germination or seedling emergence detected.

Typically, light reduction reduces *Zostera* flowering success (Bulthuis, 1983; Dennison et al., 1987; van Lent et al., 1995), although Phillips and Backman (1983) observed 100% flowering in annual *Z. marina* growing across a wide depth gradient extending from the intertidal to a depth of seven meters below low water in the Sea of Cortez, Mexico. They also observed that plants growing in deep water (7 m) flowered and produced mature seeds that were released much earlier than those of plants growing in shallow water (<3 m). Plants in intertidal locations were the most delayed in their reproduction. In contrast, Orth and Moore (1983b) found little flowering in perennial *Z. marina* growing near its depth limits in the Chesapeake Bay.

Interactions between light availability and other factors such as nutrient availability on flowering success in *Zostera* have received only limited study. Short (1983) reported higher flowering rates of *Z. marina* growing in shallow, nutrient-poor sediments in Alaska compared to deeper, nutrient-rich sediments. van Lent et al. (1995) subsequently investigated the interaction of light and nutrients on flowering of *Z. marina* in The Netherlands. Here, they found that although light availability was the principal factor affecting flowering success, when sufficient light was available, sediment nutrient enrichment significantly increased flowering over unenriched treatments.

As discussed in section II.A, genetic investigations are beginning to reveal the nature of the phylogenetic relationships within the genus *Zostera* (Les et al., 2002; Kato et al., 2003), although several species in the genus are not yet fully investigated (Fig. 6). Indeed, a discussion continues about dividing the genus *Zostera* into two genera, *Zostera* and *Nanozostera* (Tomlinson and Posluzny, 2001; Kato et al., 2003), each with several species.

The first major geographic comparison of *Z. marina* populations demonstrates distinct genetic separation between clades in the eastern Atlantic, the Black Sea through Portugal, the western Atlantic, and the Pacific coast of North America (Olsen et al., 2004). These finding show an area of unexpectedly high genetic diversity for *Z. marina* in the North Sea-Wadden Sea-southwest Baltic Sea region. *Z. marina* likely "originated in the Pacific between 8 and 20" million years ago (Olsen et al., 2004); given that five *Zostera* species now co-occur in the northwest Pacific (Fig. 6), the genus *Zostera* may have originated in this region (Kato et al., 2003).

Recent advances in genetic techniques have allowed researchers to evaluate a great deal about the development, diversity, inter-connectivity and fitness of *Zostera* populations (Ruckelshaus, 1995, 1996, 1998; Reusch et al., 1999a,b, 2000; Reusch, 2001, 2003; Hammerli and Reusch, 2003; Olsen et al., 2004). Not only can this information be used for understanding responses of *Zostera* to natural and anthropogenic stresses, but possibly even more importantly, it is useful for management and restoration of diminished areas. For example, Reusch (2002) found that the area of genetic connectivity in a region of the Baltic was nearly double that of the northern Wadden Sea. Environmental stresses in the Baltic region might result in potentially broader impacts there, given the generally lower genetic diversity found in the north Baltic Sea. The relationship between population persistence in changing and stressful environments is not a simple one. Reusch and his associates (Reusch et al., 1999a) reported a single genotype clone extending over an area of approximately 160×40 m^2, with an estimated age of more than 1000 years, suggesting a successful broad plasticity in phenotype. Given the current capacity to identify individual clones, greater understanding of their arrangement and persistence in the landscape may allow inferences about the history or disturbance regime of a site that could prove useful for management (Reusch et al., 1999b). Similarly, improved knowledge of genetic diversity and fitness as well as understanding of the importance of inbreeding and outcrossing in *Zostera* populations (Ruckelshaus, 1995) can provide important information

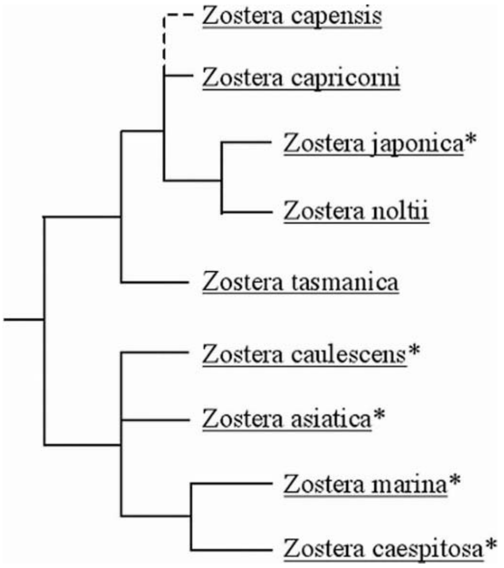

Fig. 6. Phylogenetic tree of the genus *Zostera* based on Les et al. (2002) and Kato et al. (2003). Dotted line indicates tentative species relationship; branch length is arbitrary. Family divisions within the Zosteracea are still under discussion. *Show species co-occurring in the northwest Pacific.

for restoration (Williams and Orth, 1998; Olsen et al., 2004).

III. Ecology

A. Ecological Functions

Zostera beds in general provide a wide array of ecological functions important for maintaining healthy estuarine and coastal ecosystems, creating essential habitat, and forming a basis of primary production that supports ecologically and economically important fisheries (Duarte et al., in press). *Zostera marina* provides habitat for numerous commercially important fish and shellfish species (Orth and Heck, 1980; Thayer et al., 1984; Orth and van Montfrans, 1987; Heck et al., 1989, 1995, 2003; Fredette et al., 1990; Short et al., 1993a; Dean and Haldorson, 2000; Beck et al., 2001; Short et al., 2001). In New South Wales, Australia, areas vegetated with *Z. capricorni* were found to have the greatest diversity and highest abundance of fish in shallow, marine regions, especially during the recruitment period (West and King, 1996). These included juveniles of many commercially important species such as the yellowfin bream (*Acanthopagrus australis*) and sea mullet (*Mugil cephalus*). Worthington et al. (1995) associated the great temporal and spatial variability in juvenile species in *Z. capricorni* habitats to variability in recruitment as well as subsequent mortality. Connolly (1994a,b) reports the significantly greater abundance of fish in *Z. capricorni* (reported as *Z. muelleri*) beds compared to unvegetated habitats and suggests that the use of these *Zostera* habitats may be related to both food availability and habitat structure (see Gillanders, Chapter 21). Similarly, Woods and Schiel (1997) found that the crab *Macrophthalmus hirtipes* used only *Z. capricorni* (reported as *Z. novazelandica*) beds, especially along patch edges of the seagrass, to the exclusion of other habitats as they fed on both the seagrass and sediment in the patches. Here, their burrows affected seagrass bed structure as crab burrow abundance at patch edges accelerated patch erosion. The relationships between the *Zostera* habitats and organisms using these habitats are very complex. In mixed beds of intertidal *Z. capricorni* (reported as *Z. muelleri*) and subtidal *Z. tasmanica* (reported as *Heterozostera tasmanica*), for example, differences in fish assemblage have been related more to the depth zone of the habitat than to the presence or absence of vegetation (Jenkins et al., 1997). Similarly, abundance of some gastropods was found to be significantly different between seagrass species in mixed beds of *Z. caulescens* and *Z. marina* (Toyohara et al., 1999).

Overall, the generally recognized value of *Zostera* beds as important nursery areas for many species has not been well quantified for most regions of the world (Heck et al., 2003). Heck et al. (2003) suggest that the structural component provided by seagrass beds may be the most important attribute contributing to their nursery function. There are, however, many recent studies continuing to confirm the greater habitat functions and secondary production of *Zostera* beds compared to adjacent unvegetated areas (Fredette et al., 1990; Costa, 1994; Orth et al., 1996; Dean and Haldorson, 2000). Yet the impacts of the continuing loss of these of these important habitats to fisheries is still not well quantified (Beck et al., 2001).

Some species associated with *Z. marina* habitat are in decline, such as flounder, cod and scallops. In Puget Sound, Washington juvenile salmonids are associated with *Z. marina* habitat and are listed as threatened (http://www.nwr.noaa.gov/1salmon/salmesa/). The *Z. marina* limpet, *Lottia alveus,* became extinct after the 1930s wasting disease (Carlton et al., 1991). The brant goose (*Branta bernicla*), a species dependent on *Z. marina* as a primary food source, was abundant before the 1930s and has only partially recovered. Ducks, swans, and other species of goose use *Z. marina* as food and are known to stop in *Z. marina* areas during migration. The Pacific black brant migration is linked closely to the distribution of *Z. marina* at sites from Baja California, Mexico to Izembek Lagoon, Alaska (USA) (Wyllie-Echeverria and Ackerman, 2003). *Zostera* beds are also important foraging habitats for wading birds such as the heron (Matsunaga, 2000). The abundance of *Zostera* and waterfowl populations have been reported to co-vary in many areas. In British Columbia, Canada, expansion of *Z. japonica* habitat was associated with increases in dabbling ducks and brant (Baldwin and Lovvorn, 1994a) and waterfowl distribution within shallow water areas has been related to the presence of *Zostera* vegetation (Baldwin and Lovvorn, 1994a; Clausen et al., 1998). Conversely, the impacts of waterfowl on *Zostera* have been quantified and birds have been found to consume from a low percentage to more than half of *Zostera* biomass in areas studied

(Nienhuis, 1978; Baldwin and Lovvorn, 1994b; Portig et al., 1994; Schutten et al., 1994; Fox, 1996; Vermaat and Verhagen, 1996).

The importance of *Z. marina* to estuarine and coastal productivity was highlighted in the 1930s, when a large-scale die-off of *Z. marina* occurred on both sides of the Atlantic due to wasting disease (Rasmussen, 1977). The disease resulted in the loss of over 90% of the North Atlantic *Z. marina* population, and this loss had a catastrophic effect on estuarine productivity including the disappearance of the scallop (*Argopecten irradians*) fishery and drastic reduction in brant geese (*Branta bernicla*) populations (Milne and Milne, 1951).

In addition to functions as nursery and feeding ground, *Zostera* beds enhance the local productivity of an area through increased epibenthic and benthic production, providing substrate for epiphytes and enhancing benthic invertebrate production (Fredette et al., 1990). *Zostera* beds act as a filter of estuarine water, trapping and binding sediments (Rasmussen, 1977; Fonseca et al., 1983; Fonseca and Fisher, 1986; Fonseca, 1992; Heiss et al., 2000) and dampening wave and current energy (Grizzle et al., 1996; Koch and Verduin, 2001). These plants also take up and bind contaminants (Lyngby and Brix, 1982; François et al., 1989; Ward, 1989; Hoven et al., 1999). *Zostera* beds produce and release O_2 to the water, create and export organic material, and facilitate the accumulation of organic matter in the sediments (Costanza et al., 1997). *Zostera* is important in the nutrient cycling of the coastal ocean, increasing decomposition in the sediments, accelerating nutrient regeneration, and regulating nutrient cycles (Short, 1987; Hansen et al., 2000).

B. Disease

"Wasting disease" dramatically reduced eelgrass, *Z. marina,* populations in the 1930s along the Atlantic Coast of North America and Europe by 90% (Muehlstein, 1989). At the time, speculations about the causative agents of the wasting disease were numerous, and included pathogenic microorganisms, salinity, temperature, irradiance, drought, and oil pollution (Renn, 1934; Stevens, 1936; Short et al., 1988; Muehlstein, 1989). Recently, it was shown that the eelgrass wasting disease symptoms are caused by the infection of a marine slime mould-like protist, *Labyrinthula zosterae* Porter and Muehlstein (Short et al., 1987; Muehlstein et al., 1991) which has been reported in several species of *Zostera* (Short et al., 1987, 1993b). It has been stated that *Labyrinthula* is a secondary decomposer of senescent leaves (den Hartog, 1987; den Hartog et al., 1996). Now however, Ralph and Short (2002) have demonstrated that *L. zosterae* rapidly invades the healthy green tissue around black disease spots, impairing photosynthesis, and is a primary pathogen causing the wasting disease infection.

Wasting disease continues to affect *Z. marina* beds in North America and Europe with variable degrees of loss, though none to date as catastrophic as the epidemic of the 1930s (Short et al., 1986, 1988, 1993a; den Hartog, 1994). Wasting disease infection spreads through a population by direct leaf-to-leaf contact with an infected plant or by contact with drifting detached leaves. The symptoms of wasting disease are black-brown dots or streaks on the leaves, which expand to form patches, larger blackened spots, and longer streaks (Short et al., 1988; Muehlstein, 1989). The characteristic wasting disease spots result from enzymatic browning of *L. zosterae* infection (Vergeer et al., 1995). The area of green healthy-looking tissue around the spots is already infected with the pathogen, such that the extent of the disease infection (Burdick et al., 1993) is much greater than is visually evident (Ralph and Short, 2002). Microscopic examination of necrotic tissues has revealed rapid movement of the pathogen through tissues, penetrating internal cell walls. The "slime track" of *Labyrinthula* precedes the organism, initiating enzymatic degradation of eelgrass cells and destroying the cell cytoplasm (Muehlstein, 1992). The mechanism of mortality resulting from *L. zosterae* infection appears to be reduced photosynthetic activity (Fig. 7; Ralph and Short, 2002) that creates a negative carbon balance.

Many investigators have suggested that *Labyrinthula* infection in *Z. marina* is linked to already stressed eelgrass (Young, 1943; Tutin, 1938; Rasmussen, 1977), and it is believed healthy tissue can generally resist infection by the ubiquitous marine pathogen (Vergeer and den Hartog, 1994). However, using Koch's postulates, *Labyrinthula* has been demonstrated to be the etiological agent of the wasting disease (Short et al., 1987), and subsequent studies have demonstrated that the infectious *L. zosterae* is a host-specific pathogen transferred by direct contact of plants (Short et al., 1987; Muehlstein et al., 1988, 1991). It is clear that salinity plays a role in regulating disease activity (Burdick et al., 1993); the

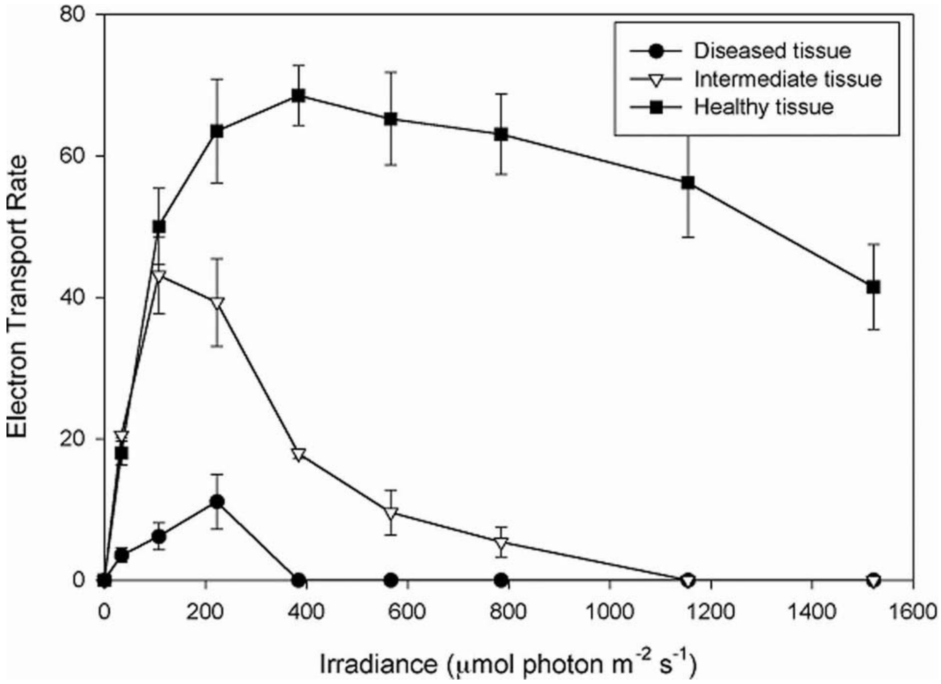

Fig. 7. PAM rapid light curves (Electron Transport Rate, ETR) of three stages of *Labyrinthula zosterae* infection on *Z. marina*: diseased (blackened), intermediate (green tissue adjacent to blackened) and healthy (green tissue away from the disease area) samples. Data are the mean ± SE ($n = 6$). Units of ETR are μmol electron m^{-2} s^{-1} and of irradiance are μmol photon m^{-2} s^{-1} (modified from Ralph and Short, 2002).

actual conditions that initiate broad-scale die-off from the disease are not understood.

Great Bay, New Hampshire, experienced a recurrence of the wasting disease in the 1980s. *Z. marina* populations went from 824 ha in 1986 to 130 ha in 1989. This loss, accounting for 80% of the *Z. marina* in Great Bay, was reversed by rapid recruitment from seed production and a recovery of *Z. marina* to 1,015 ha by 1996 (Short, unpublished).

Wasting disease symptoms and *Zostera* die-back have also been documented in other locations and species of *Zostera* around the world (Green and Short, 2003). In the 1940s, disease symptoms and *Z. marina* decline were reported from the north Pacific, in Washington and British Colombia (Watson, 1951). In New Zealand, wasting disease symptoms associated with *Labyrinthula* were reported for *Z. capricorni* in the 1960s (Armiger, 1964), and significant *Zostera* declines were observed on the north and south islands of New Zealand (Inglis, 2003). Interestingly, the first records of large-scale *Zostera* disappearance in New Zealand also occurred in the 1930s and corresponded to larger scale losses reported in southern Australia (Armiger, 1964; Inglis, 2003). In Japan, symptoms of wasting disease and the pathogen *L. zosterae* were found in *Z. caulescens* and *Z. japonica* as well as *Z. marina* (Short et al., 1993b). den Hartog et al. (1996) reported isolating *Labyrinthula* for *Z. marina* leaves in Venice Lagoon but not from co-occurring *Z. noltii,* and they concluded that there were no indications that its occurrence significantly affected the abundance of seagrass beds in that region. The impact of marine pathogens on *Zostera* populations world wide is unclear, but it is clear that *L. zosterae,* at least, plays a fundamental role in the ecology of *Z. marina* and likely other *Zostera* species.

IV. Management and Restoration

A. Anthropogenic Impacts

Loss of *Zostera* populations has been a worldwide phenomenon largely associated with anthropogenic stresses (Short and Wyllie-Echeverria, 1996, 2000). Since the arrival of Europeans in the region, the western North Atlantic has lost *Z. marina* populations

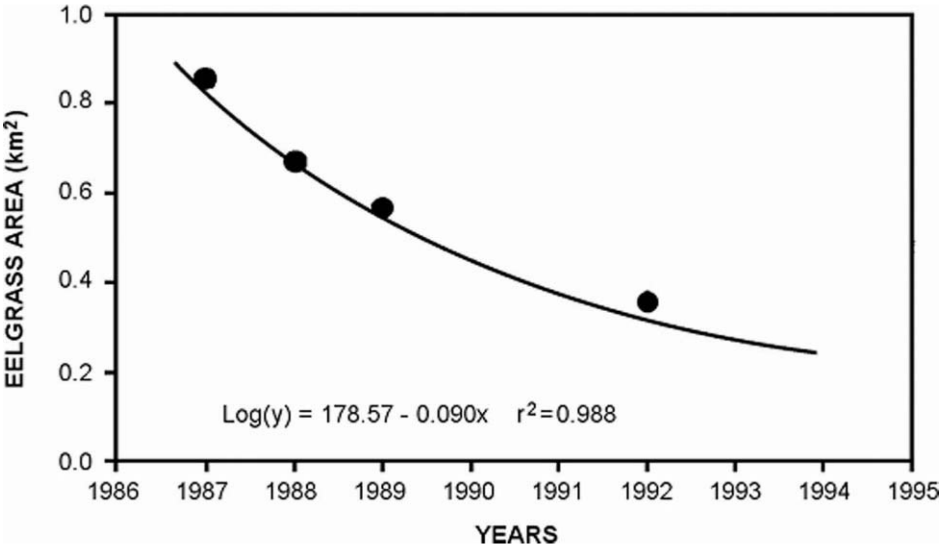

Fig. 8. Loss of eelgrass in Waquoit Bay, Massachusetts over time, with eelgrass decline resulting from number of houses in the watershed and the related, indirect impact of increased nitrogen loading (modified from Short and Burdick, 1996).

in virtually all areas of intense human settlement. By the 1970s, *Z. marina* populations along with many other oligohaline and freshwater species of submersed aquatic vegetation (SAV) in the Chesapeake Bay were at their lowest levels in recorded history (Orth and Moore, 1983a). Changes have been related to increased inputs of nutrients and sediments that have decreased light availability to these SAV populations (Kemp et al., 1983; Moore et al., 1997). Declines of *Z. marina* in Waquoit Bay, Massachusetts have been related to increased nitrogen loading (Fig. 8) that has promoted competition and/or smothering from algal growth (Short and Burdick, 1996; Bowen and Valiela, 2001). Similar impacts from direct competition with macroalgae (den Hartog, 1994; Coffaro, 1997; Hauxwell et al., 2001) and epiphytic growth (Borum, 1985) have been observed in other systems worldwide. Today, many of these areas remain devoid of *Zostera*, although, with improved sewage treatment and environmental controls of discharge as well as sediment inputs, some areas are beginning to show recovery or are now suitable for restoration (Moore et al., 2000; Short et al., 2002a). In the Grevelingen lagoon in The Netherlands, closure of the estuary to the open ocean in 1971 resulted in an initial expansion of the *Z. marina* populations followed by a significant decline (Nienhuis, 1983). In contrast to the enrichment problems experienced by *Zostera* populations elsewhere, declines of the populations here have been related to oligotrophic conditions artificially created by the closure that have resulted in temperature, salinity, low-nutrient, and disease stresses (Nienhuis, 1996).

Z. marina losses on the east coast of the US since European settlement have largely not been quantified, but north of Cape Cod, Massachusetts, loss of eelgrass is estimated to be in the order of 20%, while south of Cape Cod where the coast is more heavily populated and industrialized, as much as 65% of *Z. marina* has been lost (Short and Short, 2003). Despite fluctuations in some areas due to recent episodes of wasting disease and recovery, the trend over the past 30 years has been a steady decrease in *Z. marina* distribution and abundance due to anthropogenic impacts along the east coast of the US. In the few areas of this region where habitat change analysis has been carried out, dramatic declines in *Z. marina* populations have been documented (Orth and Moore, 1983a; Short and Burdick, 1996; Short et al., 1996). In the US, there is quantitative documentation relating rapid decline of *Z. marina* populations to anthropogenic nutrient loading by way of contaminated groundwater discharge: Waquoit Bay, Massachusetts, and Ninigret Pond, Rhode Island. In Waquoit Bay, the decline in *Z. marina* associated with nitrogen loading rates was documented in a space-for-time substitution of seven sub-estuaries having varying degrees of housing development (Short and Burdick, 1996). The greatest *Z. marina* loss occurred in the sub-estuaries with the most development; overall, 60% of the *Z. marina* was lost from this estuary in five years. In Ninigret Pond, *Z. marina* distributions were compared over a 32-year period using historical and recent maps; areal distribution of *Z. marina* declined by 41% (Short et al., 1996).

The seagrass decline in Chesapeake Bay has been attributed to the combined effects of cumulative anthropogenic stresses over many decades and a large tropical storm (Agnes) in 1972 that caused a pulsed input of nutrients and sediment from the watershed into the estuary (Kemp et al., 1983; Orth and Moore, 1983a, 1984). In addition to changing distributions in areas where *Z. marina* has not died out completely, the outer depth limits of the seagrass in the bay have decreased approximately 0.5 m over time. In one major sub-estuary, the York River, historically (1950s) the depth limits of *Z. marina* ranged from approximately 2.0 m (mean low water) at the mouth of the estuary, to 1.5 m in the middle estuary and 1.0 m at its former upriver limits of distribution (Moore et al., 2000). Current depth limits at these locations are approximately 1.5 m, 1.0 m and 0.0 m (mean low water) respectively. This change in depth limits suggest a decrease in light availability either through increased water column turbidity or epiphyte accumulation. Complete loss in upriver areas suggests that other factors may be limiting seagrass growth at the shallowest depths. Moore et al. (1997) found that pulsed turbidity levels in the spring correlated with the dieback of transplants in this region. These increases in turbidity could be due to physical factors including sediment resuspension (Koch, 1999b) or increased watershed inputs. Other physical factors associated with low tides over these flats (Koch and Beer, 1996) may also contribute to the lack of regrowth of propagules in these areas.

Dredging, filling, marina development, boat activity, fishing practices, hardening of the shoreline and anthropogenic nutrient and sediment discharge all continue to impact *Zostera* and other seagrass habitats and areas where they could return (Short and Wyllie-Echeverria, 1996; Burdick and Short, 1999; Kendrick et al., 2000). In Maquoit Bay, Maine, USA, dragging for mussels in 1999 created a 31.8 ha bare area in the center of a large *Z. marina* meadow (Neckles et al., 2005). Similar direct impacts to *Zostera* beds have been documented elsewhere including clam dredging in Maryland and Virginia, USA (Orth et al., 2002), mussel and cockle harvesting in the Dutch Wadden Sea (De Jonge and De Jong, 1992), and scallop dredging (Fonseca et al., 1984) and clam harvesting (Peterson et al., 1983) in North Carolina, USA. Recovery times have not been well documented, although in Maryland and Virginia the recovery time for *Z. marina* beds exceeded three years (Orth et al., 2002) and in Maine, complete recovery from dragging was predicted to take over 17 years (Neckles et al., 2005). Bare areas created by the dredging were also reported to experience increased erosion due to ray foraging activities and other physical forces (Fonseca et al., 1984; Orth et al., 2002) that may have inhibited recovery. Similarly, recovery of *Z. capricorni* from human impacts in Moreton Bay, Australia was slowed by low levels of grazing by dugongs (Preen, 1995).

Shellfish farming as well as other sources of excessive organic enrichment have resulted in both anoxia and sediment reducing conditions that impact *Zostera* beds (De Casabianca et al., 1997; Flindt et al., 1997; Terrados et al., 1999). Not only do hypoxic/anoxic events affect faunal communities in these vegetated habitats (Guerrini et al., 1999), but anaerobiosis as well as accompanying elevated sediment sulfide levels affect *Zostera* growth and survival through effects on root metabolism (Smith et al., 1988), nutrient uptake (Pregnall et al., 1984) and photosynthetic processes (Goodman et al., 1995).

B. Use of Zostera Species as an Indicator

The establishment of relationships between light availability, water quality conditions and depth distribution of a widely distributed species such as *Z. marina* (Dennison and Alberte, 1985; Duarte, 1991, Olesen, 1996) has provided an important tool for establishing habitat requirements for the species, and subsequently using the distribution or presence/absence of the species as an indicator of environmental conditions or health of a system (Dennison et al., 1993; Short et al., 1993a). In the Chesapeake Bay region, for example, habitat requirements for polyhaline regions of the Bay (Table 2) were established based upon seasonal medians of water quality constituents (light attenuation, total suspended solids, chlorophyll *a*, dissolved inorganic nitrogen and dissolved inorganic phosphorus) that characterized the local environments of areas with either fluctuating or persistent beds of *Z. marina* or the survival of *Z. marina* transplants (Batiuk et al., 1992). Subsequently, water clarity requirements for

Table 2. Habitat conditions suggested for management of *Zostera marina* in Chesapeake Bay, USA and its tidal tributaries (modified from Kemp et al., 2004).

		Primary requirement[a]	Secondary requirements[b]					
Salinity regime[c]	Growing season[d]	Minimum light requirement (%)	Water column light req. (%)	Water column light atten (K_d, m^{-1})	Total susp. solids (mg l^{-1})	Plankton Chl-*a* (μg l^{-1})	Diss. Inorg. Nitrgn (mg l^{-1})	Diss. Inorg. Phos. (mg l^{-1})
Polyhaline	Mar–May Sep–Nov	>15	>22	<1.5	<15	<15	<0.15	<0.01

[a] Minimum light requirement for *Z. marina* survival as a Percent of surface Light at Leaves (PLL).
[b] Relationships were derived from statistical analyses of field observations on water quality variables in comparison to *Z. marina* distributions at selected sites (Batiuk et al., 1992; Dennison et al., 1993). Water column light requirement calculated from light attenuation coefficient (K_d) assuming exponential attenuation and 1 m water column.
[c] Regions of the estuary defined by salinity regime. Polyhaline = >18 psu.
[d] Medians calculated over this growing season should be used to check the attainment of any of these habitat requirements, and raw data collected over this period should be used for statistical tests of attainment. For polyhaline areas, the data are combined for the two periods shown.

Z. marina were established. At the leaf surface (i.e. after penetration through the epiphyte layer), light equal to approximately 15% of surface irradiance is needed for *Z. marina* survival, which is equivalent to 22% of surface irradiance at its maximum depth of survival in this region (Kemp et al., 2004). These water-quality habitat requirements sufficient to support survival, growth and reproduction of seagrass are then used as criteria to assess the environmental conditions in the system. As *Z. marina* depth limits increase, turbidity and epiphytic accumulations decrease. Empirical models are used to estimate epiphyte accumulations, and therefore the percent light at the leaf surface, based on inorganic nutrient levels and suspended particle concentrations (Batiuk et al., 2000; Kemp et al., 2004). The degree of attainment of seagrass habitat requirements in any polyhaline area of the Bay region serves as an index of overall environmental condition. In Australia, correlations between water quality parameters and seagrass depth penetration for *Z. capricorni* were developed for use as indicators of water quality in Moreton Bay, (Abal and Dennison, 1996). Here, highest correlations were observed between light attenuation coefficients, total suspended solid concentrations and chlorophyll *a* levels and the maximum depth of seagrass penetration.

Although excessive nutrient enrichment of systems has been related to seagrass declines, presently there are few tools available for early assessment of potential system impacts. One approach that has been investigated is to use *Z. marina* plant morphological characteristics and tissue nutrient constituent levels to estimate nutrient availability (Lee et al., 2004). Here, *Z. marina* growing along gradients of nutrient conditions was sampled in three New England estuaries in the US (Great Bay Estuary, Narragansett Bay, and Waquoit Bay). *Z. marina* leaf nitrogen (N) content was significantly higher in up-estuary sampling stations than stations down-estuary, reflecting established environmental nitrogen gradients. But leaf N content alone showed high variance, limiting its ability to discriminate the early stages of eutrophication. In order to find a stronger indicator, plant morphological characteristics such as number of leaves per shoot, blade width, and leaf and sheath length were examined, but they only weakly correlated with leaf tissue N content. However, leaf mass (mg dry wt cm^{-2} leaf area) exhibited a strong and consistently negative relationship with leaf tissue N content, and the ratio of leaf N content to leaf mass was a more sensitive and consistent indicator of early eutrophication than either characteristic alone. The feasibility of using this particular relationship in *Z. marina* leaves as a nutrient pollution indicator (NPI) was demonstrated.

Recent advancements in technology now permit the rapid, in situ, detection of physiological stress at the photosynthetic level in seagrasses using pulse-modulated fluorescence (PAM) techniques (Falkowski and Raven, 1997; Larkum et al., Chapter 14). Since environmental stresses can affect PSII reaction centers (Ralph, 1999), fluorescence can be used as a tool in quantifying stress response as demonstrated in *Z. capricorni* (Haynes et al., 2000; Macinnis-Ng et al., 2002, 2003) and *Z. marina* (Ralph and Short, 2002). The advantages of PAM techniques are their ability to detect photosystem characteristics non-invasively (Larkum et al., Chapter 14). PAM techniques are potentially very useful in providing rapid assessment of the quality and health of *Zostera* systems for management purposes. However their application in the field still requires a great deal of development and testing.

C. Monitoring

Zostera distribution and health has been monitored through both aerial and ground assessments more than any other genus as a result of the ongoing and long-standing focus on *Z. marina* in Europe (Boström et al., 2003; Hily et al., 2003), North America (Koch and Orth, 2003; Short and Short, 2003; Wyllie-Echeverria and Ackerman, 2003) and Asia (Aioi and Nakaoka, 2003; Lee and Lee, 2003). Until recently, only localized monitoring, often with varying methodology, has been done. Little to no long-term monitoring has been done on the other eight *Zostera* species. Global monitoring of seagrasses has begun (www.SeagrassNet.org), but for *Zostera* these efforts are still limited. Repeated monitoring yields knowledge on the time course of change in seagrass habitat (Moore et al., 2000; Burdick and Kendrick, 2001) and could provide comparative information on *Zostera* species from around the world. In order to assess the magnitude of anthropogenic impacts and distinguish the signature of global climate change (Short and Neckles, 1999), long-term, comparable monitoring efforts are critical.

D. Restoration

The environmental factor with the greatest impact to seagrass habitats worldwide is the reduction in water clarity that results from anthropogenic inputs to coastal waters (Short and Wyllie-Echeverria, 1996). Improvement of water clarity is the single greatest factor that will aid in the restoration of *Zostera* species. Obviously, reduced anthropogenic inputs through reduction in nutrient loading and elimination of sediment discharge into coastal waters will result in improved water clarity. Such improvements in water clarity will allow *Zostera* to begin to reestablish its former distribution and achieve historical depth limits. The current trends in human population growth and distribution make achievement of these goals an extreme and costly challenge requiring major financial input, political will, and environmental awareness. Locally, reduction in nutrients and sediments that enter into the system and increased flushing in restricted lagoons and harbors can improve water clarity. Unfortunately, cleanup efforts will require long-term commitments because of cost and because changes to land use practices take time to implement and ground water residence time in coastal systems can be decades or longer (Phillips et al., 1999; Robinson and Reay, 2002).

Since *Zostera* species and other seagrasses have the capacity to improve water clarity in their local environment by promoting particle settlement, reducing re-suspension and taking up nutrients (Kemp et al., 1984; Ward et al., 1984; Fonseca, 1996; Koch, 1999b), once plants are lost from a system, water quality requirements for recovery may actually be greater that those needed for maintenance of existing populations (Kemp et al., 2004). Similarly, propagule supply of both vegetative material and seeds in established beds may provide a greater capacity for recovery from episodic stresses (Orth and Moore, 1986; Guerrini et al., 1999) than areas with no established plants that have to rely on seeds or propagules from other areas (Orth et al., 1994; Harwell and Orth, 2001, 2002, Orth et al., Chapter 5).

Most seagrass restoration has occurred in *Z. marina* habitat and has progressed from early transplant efforts (Phillips, 1974; Fonseca et al., 1982) to more scientific investigations of site selection and transplant methodologies (Fonseca et al., 1998; Calumpong and Fonseca, 2001; Short et al., 2002a). *Zostera* restoration-science efforts now include rigorous methodology for fulfilling the statutory requirements for compensatory mitigation to offset impacts to the seagrass (Davis and Short, 1997; Fonseca et al., 1998) and simplifying the techniques, reducing the costs, and developing procedures that community-based volunteer groups can use to embrace the task of revitalizing the coastal environment (Short et al., 2002b). Both mitigation and community-based restoration are important and needed to slow the loss of seagrass habitat and reverse the trend of coastal ecosystem degradation. Much of the information in restoration science has come from work on *Z. marina* (Table 3).

The scientific tools for *Zostera* are: (a) a quantitative site selection model (Short et al., 2002a); (b) a protocol to identify a sustainable source

Table 3. Zostera restoration projects. Sites include full scale transplant efforts (hectares) and test transplants less than 0.01 ha per location (T). Expanded from Short et al. (2002a).

Location	Project	Sites attempted	Sites successful	Area planted	Source
Netherlands	Wadden Sea	3	2	T	Hily et al. (2003), van Katwijk (2000)
Maine	Wells NERR Project	2	0	T	Short et al. (1993a)
New Hampshire	NH Port Mitigation Project	5	2	2.52 ha	Short et al. (2002a)
	NH TERFS Method Development	6	2	T	Short et al. (2002b)
	US ACE Dredging Mitigation	3	2	2 ha	Davis and Short (2003)
Massachusetts	NOAA New Bedford Harbor Project	4	2	0.8 ha	Kopp and Short (2000), Short et al. (2002a)
	EPA Boston Harbor Project	2	0	T	Chandler et al. (1996)
Rhode Island	RI Aqua Fund Project	6	1	T	Kopp et al. (1994), Kopp unpublished
	NOAA World Prodigy Mitigation	10	2	T	Fonseca et al. (1997); Fonseca (personal communication)
	RI DEM Narragansett Bay Project	2	0	T	Adamowics (1994).
	Save the Bay Wickford Harbor	1	1	T	Richardson (personal communication)
	NOAA/NERR Seeding Project	3	1	T	Granger (personal communication)
Connecticut	Niantic River Pilot Eelgrass Restoration	1	1	0.04 ha	Short (1988)
New York	NY Sea Grant, Great South Bay Project	1	1	T	Churchill et al. (1978)
New Jersey	NOAA/NMFS Raritan Bay Project	5	0	T	Reid et al. (1993).
Maryland	Chesapeake Bay and Maryland Coastal Bays	<10	<5	T	MD DNR (unpublished)
Virginia	Chesapeake Bay and Virginia Coastal Bays	<30	<15	T and 100 ha.	Orth (personal communication)
North Carolina	Beaufort area	5	5	T	Fonseca et al. (1982)
	Back Sound	1	1	T	Kenworthy et al. (1980)
California	Mission Bay	6	6	3.5	Hoffman (1988)
	San Diego Bay	5	2	6.8	Merkel and Hoffman (1990)
	San Diego Bay	5	?	1.62	Goforth and Peeling (1980)
	San Francisco Bay	3	?	T	Fredette et al. (1988)
Pacific Northwest	Review—CA, OR, WA, BC	17	11	T	Thom (1990)
British Columbia	Strait of Georgia	4	4	T	Harrison (1990)
Japan	Review—Japan			T	Terawaki et al. (1999)
	Sea of Japan			T	Tamaki et al. (1999)

of planting stock; (c) a reliable planting method (Davis and Short, 1997; Orth et al., 1999; Granger et al., 2000; Short et al., 2002b); and (d) a mechanism for identifying the outcome of the restoration (Fonseca et al., 1998; Short et al., 2000). Likely, the most important tool is site selection (insuring adequate water clarity, low bioturbation, and appropriate sediment and physical conditions) for both mitigation and community-based restoration (Burdick-Whitney and Short, 2002). Identifying a sustainable planting stock (be it shoots or seeds) is necessary and requires painstaking sustainable harvest of mature shoots or a technique that collects seeds without adversely impacting recruitment to natural beds. Successfully used planting methods for *Z. marina* include TERFS (Transplanting Eelgrass Remotely with Frame Systems, Short et al., 2002b), the use of simple un-anchored (Orth et al., 1999) or anchored shoots (Davis and Short, 1997), and seeding by hand (Harwell and Orth, 1999) or by machine (Granger et al., 2000). Determining success of *Zostera* restoration requires rigor and demonstrated replacement of habitat function for mitigation vs. observed persistence of the planted area for community activities. The importance of restoration science to the success of community based restoration and compensatory mitigation is clear, but the success of any efforts to transplant or seed new *Zostera* populations will depend on adequate water quality conditions being re-established.

V. Future Research Needs

The genus *Zostera* has received much attention in all aspects of scientific investigation, resulting in part from its distribution in the temperate, developed areas of high human populations and academic focus. Particularly *Z. marina* has a tremendous body of research on its ecology, distribution, and physiology. The other eight *Zostera* species are now receiving more attention, but our understanding of their ecology and physiology is far from complete. As our knowledge base of these species increases, broader comparisons can be made that will help to improve management of each.

Despite extensive work in other areas, little is known of the genetics of *Z. marina*, and, surprisingly, genetic investigations of other species are often more advanced. Such investigations, especially of the perennial and annual forms of *Z. marina*, along with further studies of field ecology and distribution, will in time yield a better knowledge of the genus *Zostera* and its evolution.

Assessment and monitoring of the distribution of all *Zostera* species is needed to document the losses that are occurring and to provide support to reverse these declines and restore these seagrass beds. In many parts of the world, *Zostera* beds are being lost due to reduced water clarity and direct human impacts even before documentation of their existence has been made. Monitoring requires long-term consistent effort but yields valuable information on incremental changes that otherwise may escape perception. Other losses related to the wasting disease have occurred and are continuing to occur in *Z. marina* and other *Zostera* species. The extent and etiology of wasting disease and its relation to the ecology of *Zostera* needs more investigation.

Zostera has been shown to have potential as an indicator of estuarine and coastal system health. More work is needed to refine existing, and develop new, environmental indicators involving *Zostera.* Beyond additional research, greater efforts are needed to increase public awareness of the importance of *Zostera* populations and the critical role they play in the ecology of coastal oceans and in their contribution to fisheries resources.

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Chapter 17

Biology of Posidonia

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I. Introduction

At least 17,000 km separate the endemic Mediterranean *Posidonia oceanica* (L.) Delile from the eight other species of the same genus (*P. angustifolia* Cambridge and Kuo, *P. australis* Hooker, *P. coriacea* Kuo and Cambridge, *P. denhartogii* Kuo and Cambridge, *P. kirkmanii* Kuo and Cambridge, *P. ostenfeldii* Den Hartog, *P. robertsoniae* Kuo and Cambridge, and *P. sinuosa* Cambridge and Kuo) (Cambridge and Kuo, 1979; Kuo and Cambridge, 1984). Along Mediterranean coastlines, *P. oceanica* covers about 2% of the seafloor. Australian *Posidonia* occurs in benthic habitats covering about twice the area of the Mediterranean Sea.

The nine members of the genus *Posidonia* are perennial plants, with linear leaves and a persistent leaf-sheath after the leaf-blade has been shed. They are monoecious, and have hermaphrodite inflorescences. The perianth is absent (Den Hartog, 1970). The genus consists of large seagrasses with long leaves, high shoot and leaf longevities, and low shoot

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turnover compared to the other seagrass (Duarte, 1991; Marbà and Duarte, 1998; Marbà and Walker, 1999; Hemminga and Duarte, 2000). Kuo and den Hartog (2001) provide a good overview of all *Posidonia* species; see also, Kuo and den Hartog, Chapter 3 and Mateo et al., Chapter 7.

According to a review of the literature on seagrass ecology (Duarte, 1999), about 600 papers have been published in this area between 1989 and 1997. One of every four papers on the biology and ecology of all seagrass species was devoted to *P. oceanica*. Thus Mediterranean beds have been studied more extensively than those of the Australian species of the genus. The number of international papers on *Posidonia* spp. is rapidly increasing, but there is still a paucity of papers devoted to the comparison of the two different biogeographic regions.

This chapter describes *Posidonia* species and ecosystem dynamics in relation to key ecological processes and functions. We illustrate similarities and differences between Mediterranean and Australian *Posidonia* ecosystems.

II. Systematics

On the basis of ecological, vegetative, and reproductive characteristics, nine seagrasses have been classified in the genus *Posidonia* (Den Hartog, 1970). Eight species occur in Australian coastal waters (*P. angustifolia*, *P. australis*, *P. coriacea*, *P. denhartogii*, *P. kirkmanii*, *P. ostenfeldii*, *P. robertsoniae*, and *P. sinuosa*) (Cambridge and Kuo, 1979; Kuo and Cambridge, 1984). One species, *P. oceanica*, is endemic to the Mediterranean Sea (Den Hartog, 1970; Phillips and Meñez, 1988).

Recent morphological and preliminary genetic studies (Campey et al., 2000) emphasized the considerable overlap in vegetative characters (leaf widths, epidermal cell dimensions, sheath lengths) used by Kuo and Cambridge (1984) to distinguish species of the *Posidonia ostenfeldii* group at sites in southwestern Australia and the need for further research to resolve species boundaries. There is also need for further investigation of the use of microsatellites to determine the degree of difference that may exist in *P. oceanica*.

III. Distribution of the Genus

The disjunct distribution of *Posidonia* is striking (Fig. 1). *P. oceanica* is restricted to the Mediterranean Sea, whereas the other eight species of *Posidonia* occur across southern Australia (Short et al., 2001; den Hartog and Kuo, Chapter 1). Genetically, Mediterranean and Australian species of *Posidonia* are not close. The divergence in their DNA sequences (Waycott and Les, 2000) indicates that the separation of the two groups took place at a relatively early time in the history of the seagrasses, probably during the Late Eocene. The origins of the genus are postulated to have been in the Tethys Sea, but reconstructions of the position of shallow seas at that time are not convincing as potential seagrass habitat (Hemminga and Duarte, 2000).

The beds in the Mediterranean Sea (Fig. 1) cover a surface area of 25,000–50,000 km^2 representing 1–2% of the total surface (Pasqualini et al., 1998). The western distributional limit of *P. oceanica* is associated with the Almeria–Oran density front (boundary between water masses of different density which separates the Atlantic from the Mediterranean surface waters; 250 km eastward from Gibraltar strait) (Marbà et al., 1996). The eastern distribution limit is more eastwards in the Northern coast than in African coast. Beds are less widespread in the eastern basin and are not recorded along the coasts of Lebanon, Israel, and Syria. In terms of depth limits, *P. oceanica* meadows are recorded from 0.5 to 40 m (Boudouresque and Meinesz, 1982; Pergent et al., 1995), and living plants have been found at 48 m depth (Augier and Boudouresque, 1979). In turbid waters, the lower limit of the beds is of the order of 9 m (Pergent et al., 1995). In many inshore areas of the Mediterranean, *P. oceanica* is widespread but disappears near river mouths where the input of fresh water and fine sediments is high (Rhône, Po, Nile).

Along *Australian* coasts, the genus *Posidonia* is widely distributed, from 23°S on the west coast to 32°S on the east coast (Larkum and den Hartog, 1989), a distance of more than 4,000 km (Fig. 1). With the exception of *P. australis*, Australian species of *Posidonia* occur on the temperate west and south coasts, a region characterized by microtides (<1 m), clear, warm temperate waters, an arid hinterland with low run-off and coastal geomorphology dominated by Pleistocene sediments (Kirkman and Walker, 1989; Walker, 2000). They occur at depths ranging from the intertidal to more than 35 m (Cambridge and Kuo, 1979; Kuo and Cambridge, 1984) with the deepest record of 44 m for *P. angustifolia* (Huisman et al., 1999), in sedimentary environments varying in wave exposure from sheltered embayments (e.g. Shark Bay, Cockburn Sound, Frenchmans Bay,

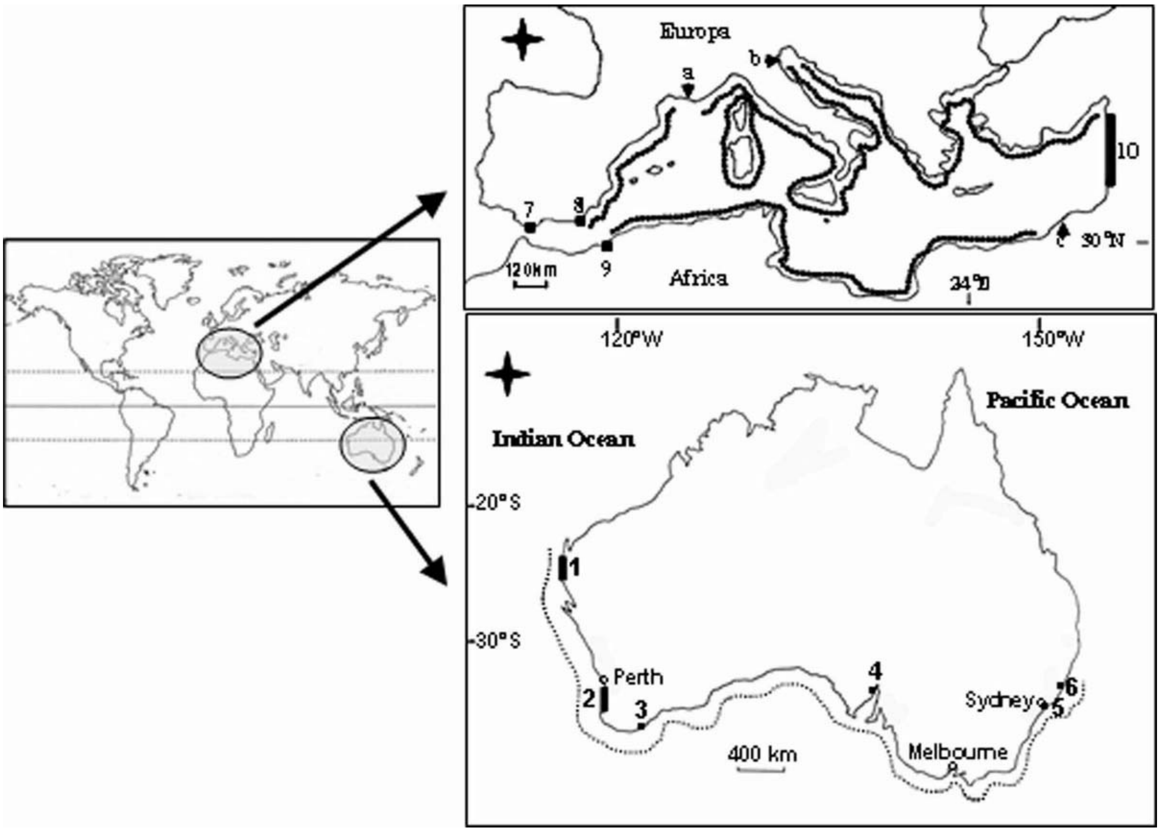

Fig. 1. Maps of Australia and Mediterranean Sea showing the *Posidonia* spp. distribution. List of locations cited in the text on Australian coasts: 1. Shark Bay and Coral Bay, 2. Cockburn Sound-Success Bank-Geographe Bay, 3. Frenchman Bay, 4. Spencer Gulf, 5. Botany Bay, 6. Port Macquarie and on Mediterranean coasts: 7. Gibraltar, 8. Almeria, 9. Oran, 10. Coasts of Lebanon, Israel and Syria; a, b, c: river mouths of Rhône, Po, and Nile, respectively.

Spencer Gulf, Botany Bay), to more exposed coastlines (e.g. Success Bank, Geographe Bay). Salinities are generally marine but two species of *Posidonia* are found in Shark Bay near their north-western limit at salinities from marine to hypersaline (35–55‰). Salinity exerts a primary control on the distribution, productivity, and biomass of these species in Shark Bay (Walker, 1989) with productivity and biomass reduced at salinities higher than 42, similar to *P. oceanica.* The southeastern corner of Australia marks a transition zone from oligotrophic, microtidal coasts to a region with larger tides and a less arid hinterland. *P. australis* extends up the east coast to Port Macquarie, occupying lagoons and estuaries but is absent from open coast marine habitats (West et al., 1989). On the west coast, *P. coriacea* extends into the tropics at Coral Bay (23°S).

The Australian *Posidonia* species fall into two distinct groups which can be separated on the basis of their leaf and rhizome characteristics, but which also differ in their ecological characteristics. For convenience, the species described first were used to name each group, viz. *P. australis* and *P. ostenfeldii*. The *P. ostenfeldii* group of species (Fig. 2) (*P. coriacea*, *P. denhartogii*, *P. kirkmanii*, *P. ostenfeldii*, *P. robertsoniae*) is typically found in open ocean or rough water sublittoral habitats, and some aspects of their morphology and anatomy appear to be associated with surviving the strong wave movement and mobile sediments characterizing these habitats (Kuo and Cambridge, 1984; Cambridge and Lambers, 1998). All the species have long (up to 120 cm), tough leaves with a leathery texture when fresh. The leaf-bearing apices of the rhizomes are usually deeply buried (15–20 cm) so that the leaf-sheaths are correspondingly long. The rhizomes have a fan-like appearance, with predominantly vertical growth. Branching tends to occur along one plane, with the growing points maintained at a similar depth, which, together with very narrow branching angles,

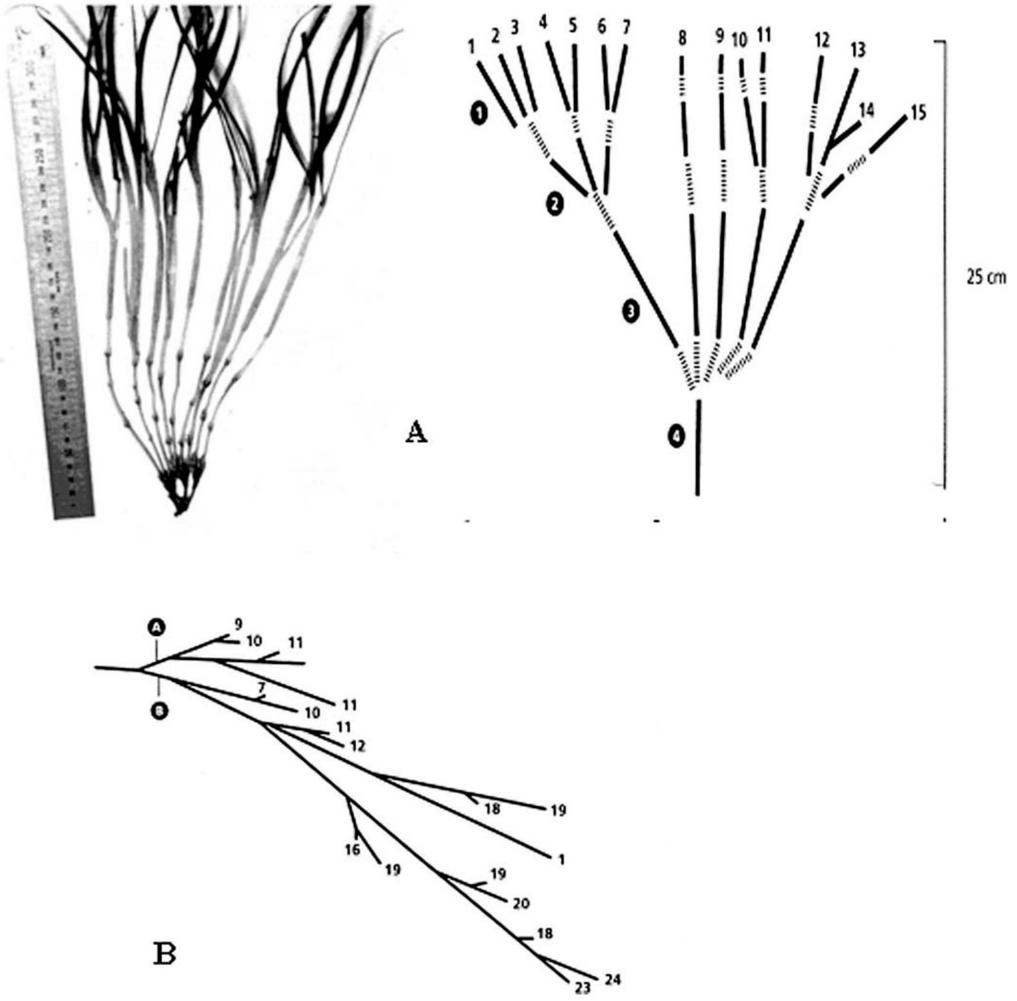

Fig. 2. (A) vertical rhizome growth typical of species of the *Posidonia ostenfeldii* group: *P. coriacea*, with phases of rapid vertical growth numbered 1–4. Shoot bearing rhizome apices numbered 1–15; (B) horizontal growth typical of species of *Posidonia australis* group, showing differential rates of growth on different axes, A and B. Numbers show nodes produced since the axes formed at the rhizome apex, ranging from 9 to 11 on *A* axis to 11–24 on *B* axis (*P. angustifolia*), from Cambridge (1999).

produces characteristic dense clumps of shoots, arranged almost linearly and with a slow rate of expansion. The *P. ostenfeldii* group of species are not usually bed-forming and instead tend to occur in isolated clumps separated by bare sand. The roots are usually long (to 40 cm), with wrinkled, expanded portions as much as 3 mm thick, and little branched.

In contrast, the *P. australis* group of species (*P. angustifolia*, *P. australis*, *P. sinuosa*) are found in more sheltered waters. They have thinner leaves, finer roots, and usually shorter leaf-sheaths, so that the growing points are less deeply buried (Cambridge and Kuo, 1979; Cambridge and Kuo, 1982). These species are usually bed-forming, filling available space with shoots by horizontal expansion of the rhizomes. In the case of *P. sinuosa*, the bed consists of very densely packed shoots (up to 1,200 shoots m^{-2}) in rows 30–40 cm wide, which alternate with strips of bare sand (Cambridge and Kuo, 1979; Smith and Walker, 2002). The rows are aligned with the dominant wave direction. Rhizome growth in each species may be rapid (15–30 cm $year^{-1}$) and is predominantly horizontal provided there is adequate space (Kendrick et al., 2002). A switch to vertical growth occurs if sand accretion is rapid or space is restricted. There appears to be a distinct differentiation in growth rate depending on whether the axis is formed from a branch or is a continuation of the main axis.

IV. Development of Meadows and Patches

A. *Posidonia oceanica in the Mediterranean Sea*

In the Mediterranean Sea, *P. oceanica* forms monospecific meadows with different types of coverage pattern (continuous to patchy with leopard-skin, in row distributions) (Molinier and Picard, 1952; Borg et al., 2005) with shoot densities ranging from meadows where densities range between 150 and 300 shoots m^{-2}(very sparse bed) to more than 700 shoots m^{-2}(very dense bed) (Giraud, 1977a). The shoots (Fig. 3) are borne by rhizomes growing either vertically (orthotropic rhizome), avoiding burial, or horizontally (plagiotropic rhizome), enabling colonization. The leaves act as sediment-traps accumulating inorganic and organic particulate matter (Dauby et al., 1995; Gacia et al., 1999; Gacia and Duarte, 2001). The progressive silting and the two types of rhizome growth result in a typical terraced formation called 'matte' consisting of the intertwining of various strata of rhizomes, roots, and sediment. In shallow waters, such an accumulation of material raises the bed to the surface. Refractory organic material remains with little alteration for millennia, with an average accretion rate of 0.175 cm $year^{-1}$, the age of the debris accumulated in this matte ranges between 0 and more than 3,000 years (Matéo et al., 1997; Mateo et al., Chapter 7). This phenomenon has been used as a record of bed history (Calmet et al., 1988; Pergent-Martini and Pergent, 1995; Hemminga and Mateo, 1996; Matéo et al., 1997).

The rhizomes grow horizontally until space has been completely colonized. The beds have wide spacing between many vertical shoots with few horizontal apices (Boudouresque and Meinesz, 1982).

The *P. oceanica* bed is the climax community of a successional process (Molinier and Picard, 1952; den Hartog, 1977). The development of the bed seems to need a substratum rich in organic material. Pioneer species such as *Caulerpa prolifera* settle, together with small phanerogams of the genera *Cymodocea* and *Zostera* can produce suitable sediments for seed germination or shoot growth. Settlement, growth, and multiplication of *P. oceanica* shoots reduce the light intensity at the seafloor which causes the mortality and the disappearance of the pioneer species (Boudouresque and Meinesz, 1982).

P. oceanica requires stable environmental conditions, preferring a coarse-grained sandy substratum but ranging from soft substrata (from fine sand to pebbly, but not muddy sediments) to rock (Mazzella et al., 1993; Bellan-Santini et al., 1994). It is stenohaline, and is not present when salinity is below 33 ppt. In the Eastern basin, *P. oceanica* can endure salinities over 40, the hypersaline environment does seem to provide optimum growth conditions (Pergent and Zaouali, 1992) but experimental work indicated significant deleterious effects over 39 (unpublished data). The tidal range is very small (20 cm as a mean) and water levels are often more influenced by barometric pressure than by tides, as is also true of southern Australia. *P. oceanica*, like its Australian relatives, is not an intertidal species and is not resistant to desiccation, but does tolerate a wide range of temperatures (9–29°C) (Boudouresque and Meinesz, 1982).

B. *Posidonia Species in Australia*

Along Australian coasts, the *P. australis* group (*P. angustifolia*, *P. australis*, *P. sinuosa*) are horizontal spreaders with little vertical shoot production. *P. angustifolia* is a fast spreading species, whereas *P. sinuosa* forms dense meadows of vertically growing shoots, sometimes reaching 1,000 shoots m^{-2} (Kendrick et al., 2002). The *P. ostenfeldii* group (*P. coriacea*, *P. denhartogii*, *P. kirkmanii*, *P. ostenfeldii*, *P. robertsoniae)* grow vertically only and form clumps not meadows.

V. Biomass Dynamics and Production of the Plant

Posidonia is a long lived seagrass (4–30 years) with long leaf life-span (70–350 days), high biomass, and productivity (Pergent-Martini et al., 1994; Cambridge and Hocking, 1997; Duarte and Chiscano, 1999; Hemminga et al., 1999; Marbà and Walker, 1999).

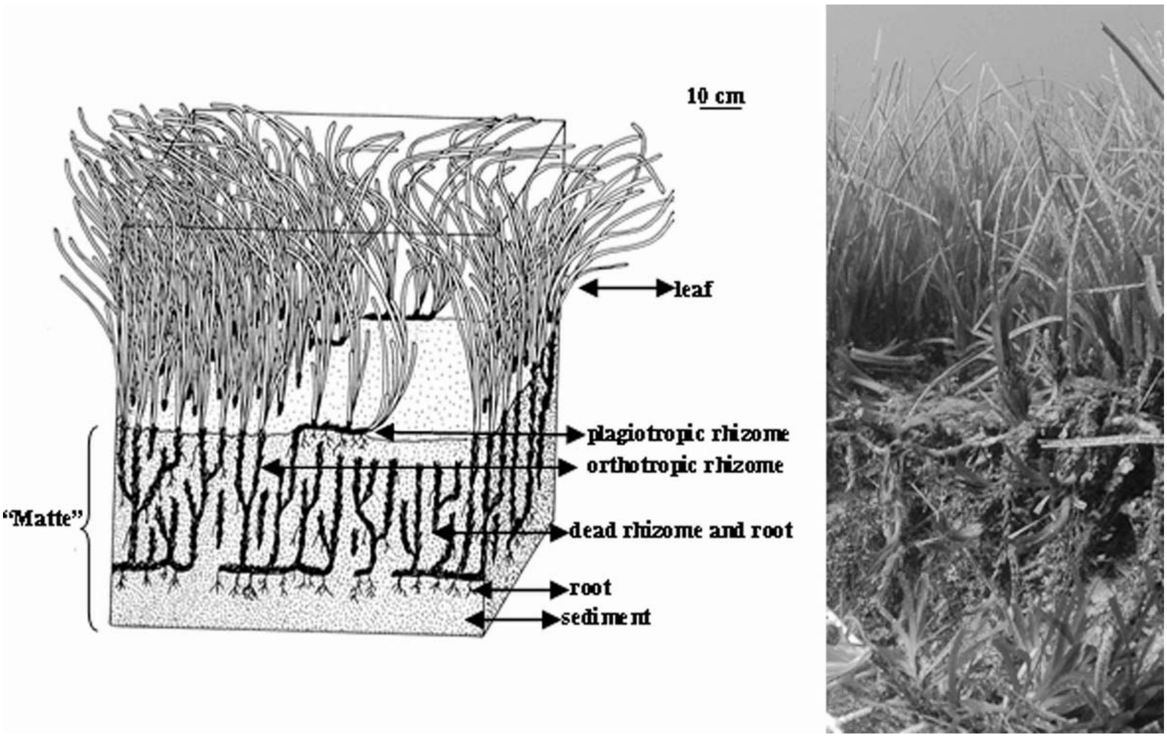

Fig. 3. Schematic illustration of the rhizomes, roots, leaves, and 'matte' in a *P. oceanica* meadow (redrawn from Boudouresque and Meinesz, 1982) and a photograph showing an actual bed).

The genus *Posidonia* exhibits differences in shoot biometry (Pergent and Pergent-Martini, 1999) (Table 1). For example, the average number of leaves (intermediate + adult leaves) per shoot and the foliar surface were greater on *P. oceanica* shoots from Calvi Bay than on *P. angustifolia*, *P. australis*, *P. coriacea*, and *P. sinuosa* shoots from Rottnest, whereas *P. oceanica* leaf widths and lengths fell within the range of values recorded for Australian species (Pergent and Pergent-Martini, 1999).

The standing crop of both above-ground (leaves) and below-ground (rhizomes and roots) of *P. oceanica* exceeds those of Australian *Posidonia* spp (Hillman et al., 1989).

In the Mediterranean Sea, *P. oceanica* beds are exposed to a broad range of light and temperature (13–26°C) and show decreasing plant growth and a marked decrease in density with depth, ranging from 1,200 shoots m^{-2} in shallow stands to fewer than 100 shoots m^{-2} at depths around 30 m. Water temperature and light vary seasonally inducing seasonal dynamics in shoot biometry and consequently on the overall biomass of the bed. Seasonal variations in shoot biometry reflect the annual cycle of leaves: appearance on the shoot, leaf fall, and growth rhythm (Bay, 1984). Juvenile leaves appear all year-round (a new leaf appears on average every 51 days; Duarte, 1991) but more leaves appear from the end of September till November. The old adult leaves necrose throughout the year but storm events induce leaf breakage and fall. The life-span of a leaf (between 7 and 12 months) depends on the month of appearance on the shoot: leaves induced at the end of the autumn and at the beginning of the winter show a longer life-span than leaves produced during other months. At 10 m depth, the turnover rates for the leaf canopy averaged over an annual cycle, was 1.1–1.8% day^{-1}(equivalent to 55–90 days for complete replacement of the canopy) (Bay, 1984; Gobert, 2002). This cycle is slightly modified with increasing depth (Caye and Rossignol, 1983; Pergent and Pergent-Martini, 1991; Buia et al., 1992). The rhizome biomass shows low seasonal variability. The shoot density (number of shoots m^{-2}) in a meadow is relatively constant throughout the year (Pergent et al., 1995). Shoot growth is highest in February and lowest in August possibly related to nutrient availability (see Romero et al., Chapter 9). The

Table 1. Biometric parameters of *Posidonia* leaves (Rottnest Island and Calvi Bay).

	P. australis	*P. coriacea*	*P. sinuosa*	*P. oceanica*
Number of adult leaves				
January	2.1 ± 0.2	1.1 ± 0.2	0.7 ± 0.2	3.0 ± 0.5
August	1.3 ± 0.2	0.6 ± 0.1	0.6 ± 0.3	3.5 ± 0.6
Length of adult leaves(mm)				
January	370.0 ± 45.2	798.1 ± 56.7	688.4 ± 50.6	250.4 ± 12.0
August	237.5 ± 18.2	552.4 ± 31.7	203.9 ± 45.8	400.9 ± 10.4
Width of adult leaves(mm)				
January	12.2 ± 0.6	4.5 ± 0.2	7.6 + 0.3	9.7 ± 0.6
August	12.8 ± 0.9	3.9 ± 0.1	6.0 ± 0.1	9.3 ± 0.6
Number of intermediate leaves				
January	1.0 ± 0.1	1.1 ± 0.1	0.9 ± 0.2	3.9 ± 0.2
August	1.0 ± 0.2	1.1 ± 0.1	1.0 ± 0.3	1.6 ± 0.4
Length of intermediate leaves(mm)				
January	120.5 ± 14.9	323.6 ± 65.0	419.0 ± 78.0	245 ± 15.0
August	119.7 ± 11.9	297.5 ± 19.1	173.5 ± 62.8	125 ± 60.0
Width of intermediate leaves(mm)				
January	12.1 ± 0.6	4.6 ± 0.2	7.7 ± 0.2	9.1 ± 0.6
August	12.6 ± 0.9	3.5 ± 0.1	5.8 ± 0.3	9.2 ± 0.4
Coefficient A per shoot (%)				
January	10.8	5.6	26.7	5.0
August	8.3	24.2	34.8	50.8
Foliar surface(cm^2 shoot^{-1})				
January	107.0 ± 15.5	59.7 ± 9.3	66.9 ± 8.5	80.6 ± 27.6
August	53.9 ± 7.3	23.3 ± 1.5	17.9 ± 4.2	280.4 ± 14.4

interannual variation of the biomass can be high and influenced by available resources (nutrients, carbon) (Alcoverro et al., 1997b) or light (Gobert, 2002).

A 10 year study of a *P. oceanica* bed (Gobert, 2002) indicated that the shoots, interconnected by rhizomes, react together. The availability of resources (e.g. light, nutrients) could explain these variations: a dense bed that is growing fast tends to increase leaf length until a factor becomes limiting, then the density decreases and the resources become available, preventing shoot mortality.

In temperate Australian waters (35°S), seasonal changes in the biomass and in primary production occur (i.e. *P. australis*, Kirkman and Reid, 1979; Cambridge and McComb, 1984; Walker and McComb, 1988; Cambridge and Hocking, 1997) with mean spring–summer biomass values higher than in winter. Turnover rates for the leaf canopy averaged over an annual cycle ranged from 1 to 1.5% day^{-1} (equivalent to 70–100 days for complete replacement of the canopy) for *P. sinuosa* and 1.5–1.9% (57–70 days) for *P. australis*. Maximum leaf growth occurs in the summer (West and Larkum, 1979). Leaf losses occur throughout the year, but were usually during spring and highest in late summer, when whole leaves were shed forming floating. Losses were also high in winter at sites exposed to winter waves (Cambridge and Hocking, 1997).

VI. Reproduction

A. Flowering Phenology of Posidonia

Flowering in the genus *Posidonia* is at most once a year with high spatial and interannual variability. Flowering phenology has been described in *P. australis* and *P. sinuosa* (Cambridge and Hocking, 1997; Smith and Walker, 2002), and *P. oceanica* (Pergent and Pergent-Martini, 1990; Buia and Mazzella, 1991; Gobert et al., 2001) (see also Kuo and den Hartog, Chapter 3). Timing of flowering is coincident (see below) in both hemispheres, which means that flowering in Australia is 180° out of phase, in terms of seasons, with that in the Mediterranean. The causes of the spatial variation in flowering frequency are presently unknown but may be influenced by genetic variation or shoot age (Balestri and Vallerini, 2003), distribution of active meristems or small-scale differences in the environment

(Marbà and Walker, 1999; Campey et al., 2002) or by temperature. Flowering occurs more frequently in shallow sites than deeper ones (Pergent and Pergent-Martini, 1988; Cambridge and Hocking, 1997). Production of reproductive shoots is an episodic phenomenon in some areas (i.e. central New South Wales, Northwestern Mediterranean) but a regular annual event on the western and southern coasts of Australia. Flowering of *P. oceanica* occurred over the entire Mediterranean basin, in 1961, 1967, 1971, 1972, 1973, 1975, 1979, 1981, 1982, and 1983 (Pergent and Pergent-Martini, 1990) and in 1994 (Sandmeier et al., 1999).

Flower buds emerge in *Posidonia* species during April–June. Anthesis begins in July continuing through to September (late winter and late summer in Australia and Mediterranean Sea, respectively), followed by fruit and seed development, with fruits being shed from November to January, depending on the species (Hocking et al., 1981, Cambridge and Hocking, 1997; Gobert et al., 2001; Smith and Walker, 2002). Flowering requires additional nutrients (Cambridge and Hocking, 1997; Gobert et al., 2005) and can affect the biometry of the flower-bearing shoot (Gobert et al., 2001). The fruits contain nutrient reserves—i.e. an accumulation of N, P, K, Ca, Mg, Na, Fe, Zn, Mn, and Cu in the developing pericarp of *P. australis* and *P. sinuosa* (Hocking et al., 1980). *P. oceanica* produces fewer flowers than other *Posidonia* species (i.e. mean flowering ratio: $<1\%$ for *P. oceanica*; 20% for *P. australis*; 3% for *P. sinuosa*; 8% for *P. coriacea*) (Pergent et al., 1997a).

In the Mediterranean, *P. oceanica* flowers rarely in the cold waters along north-western shores, whereas flowering is frequent or even annual in the southern and eastern regions of the Mediterranean basin (Molinier and Picard, 1952). Flowers and fruits of *P. oceanica* have been observed at many localities within the Mediterranean basin (Den Hartog, 1970; Giraud, 1977b; Mazzella et al., 1983; Pergent, 1985; Buia and Mazzella, 1991; Gobert et al., 2001). The establishment of seedlings is episodic. Germination begins with the development of the plumule following by the protusion of a white primary root at the radical pole, all occurring within the pericarp. There is no seed bank in *Posidonia*. After about 10 days, the apical meristem grows and produces 2 or 3 green leaves and several adventitious white roots. After 9 months, seedlings have 12–13 leaves, one primordial tap-root and 3–4 adventitious roots. At this stage, a high of mortality occurred (Balestri and Cinelli, 1995). *P. oceanica* seedlings begin to develop their own rhizome, growing horizontally at a rate of about 5–10 cm year^{-1} (Boudouresque and Meinesz, 1982). Grazing of inflorescences can affect the success of sexual reproduction (Piazzi et al., 2000).

In southeastern Australia, *P. australis* flowers infrequently (West and Larkum, 1979), associated with changes in water temperature (i.e. monthly mean temperatures 1–2°C cooler than in the previous 7 years) (Inglis and Lincoln-Smith, 1998). In contrast, *P. australis* flowers frequently in Western Australia and produces large numbers of seeds (Cambridge and Hocking, 1997; Marbà and Walker, 1996). *Posidonia* seeds deposited on unvegetated sand suffer a lower predation pressure (Orth et al., 2002). Seeds seem to play an important role in initial establishment, playing a lesser role in subsequent meadow development and maintenance in the short term compared to vigorous clonal growth. Kuo and Kirkman (1996) estimated that about 2% of seedlings survived beyond 1 year in trial plots at a site near Perth using three species of *Posidonia*. Genetic studies on *P. australis* showed populations consisting of multiclonal beds with a high degree of genetic variation, demonstrating the success of seedling establishment over longer time scales (Waycott, 1995; Waycott and Sampson, 1997).

The flowering phenology characteristics (flower structure, flower location on plant, vegetation canopy structure, longevity of flowering, pollen viability) differ from one species to another (Cambridge and Kuo, 1979; Smith and Walker, 2002). These differences may be related to different pollination strategies, e.g. low pollen dispersal, enclosed in a dense canopy, that probably induce greater neighbor–neighbor pollination for *P. sinuosa* or large pollen, dispersal above the canopy for *P. australis* (Smith and Walker, 2002).

B. Genetic Consequences

There are contrasts in the findings of the limited genetic studies of the genus *Posidonia.* For example, there is a high degree of genetic diversity within populations of the Australian *P. australis* (Waycott et al., 1997) but less genetic diversity in *P. sinuosa* (Wood et al., 1999). The genetic diversity of *P. oceanica* is very low. *P. oceanica* occurs in separate meadows that represent discrete populations with limited inbreeding (Procaccini and Mazzella, 1998; Procaccini et al., 2001). The low genetic polymorphism of *Posidonia* could be a disadvantage in facing anthropogenic pressure with potential effects on survival and expansion (Procaccini and Piazzi, 2001).

C. Recruitment

The contribution of the sexual reproduction to the maintenance and to expansion of *Posidonia* beds varies greatly between species. Sexual reproduction contributes to recruitment (Procaccini and Mazzella, 1998; Campey et al., 2002) but vegetative reproduction often maintains the meadows (Buia and Mazzella, 1991; Procaccini and Mazzella, 1998; Kirkman and Kuo, 1990; Duarte et al., Chapter 11). Recruitment of seedlings appears important for the persistence and the expansion of *P. coriacea* (Kendrick et al., 1999). Sexual reproduction varies in time as does the probability that flowers set fruits, seeds (*P. coriacea*: 21% (Campey et al., 2002); *P. australis*: 23–37% (Waycott et al., 1997); *P. oceanica*: 2%, (Balestri and Cinelli, 2003)) and finally develop new shoots. Variations in the number of flowers per inflorescence, in the number of fruits per inflorescence (Cambridge and Hocking, 1997) and in the fate of successful seeds, for example due to predation (Piazzi et al., 2000; Orth et al., 2002), are all variable. A discussion of recruitment strategies in *Posidonia* species and other genera is given by Orth et al. (Chapter 5).

VII. Dynamics of Carbon and Nitrogen

The *Posidonia* bed, as an important primary producer, is also a recognized sink for biogenic elements (Romero et al., 1992; Matèo et al., 1997; see also Mateo et al., Chapters 7 and Romero et al., Chapter 9, this volume) and could act as a sink for atmospheric CO_2 (Frankignoulle and Bouquegneau, 1987). The beds play a major role in the production (Logan et al., 1970; Walker and Woelkerling, 1988) trapping (De Falco et al., 2000) and stabilization of sediments (Boudouresque and Meinesz, 1982).

The accumulation rate of sedimentary matter in a *P. oceanica* bed (Calvi Bay–Corsica) varied over the year (average: 0.33 g_{dw} m^{-2} day^{-1}) (Dauby, 1989). The total matter flux over a yearly cycle is about 1.3 kg m^{-2}, which corresponds to a mean daily flux of 3.7 g m^{-2}. This amount of material consists of water column-originated and resuspended particles. The relative importance of each fraction changes several times during the year with respect to climatic or biological events. The measured yearly flux of settling suspended particulate matter was about 420 g m^{-2}, which corresponds to a mean daily flux of 1.2 g m^{-2}. In absence of resuspension, the canopy slightly increased particle trapping (Gacia et al., 1999); only about 10% of the matter produced in the pelagic zone sinks and reaches the bottom, probably as a result of the high grazing pressure suffered by phytoplankton in such waters (Dauby, 1989). The litter is partly exported and partly slowly degraded, but a fraction remains in the upper sediment layer and is thus easily remobilized (Dauby et al., 1995).

A. Carbon

Seagrasses are important contributors to oceanic net carbon production (Duarte and Cebrián, 1996): exceeding 15 gC m^{-2} day^{-1} in some areas (Phillips and McRoy, 1980). This organic carbon produced is important in the environment and in the food chain (i.e. Nichols et al., 1986).

Carbon metabolism has been described for seagrasses in general (Touchette and Burkholder, 2000b; Larkum et al., Chapter 14), for Australian *Posidonia* (i.e. Abel and Drew, 1989; James and Larkum, 1996) and for *P. oceanica* (e.g. Alcoverro et al., 1998, 2001a,b; Modigh et al., 1998; Mateo et al., Chapter 7). Carbon dynamics vary considerably between species, location and season.

In an eastern Australian estuary, in *P. australis* beds, 37% of the year's production sank to the bottom and was utilized by benthic detritivores, 12% was exported as floating leaves and only 3% of the production was eaten by herbivores (Kirkman and Reid, 1979). Occasionaly, accumulations of persistent organic matter may develop in sediments (Hemminga and Duarte, 2000). In Shark Bay, rates of decomposition of *P. australis* were 0.5% day^{-1} (Walker and McComb, 1985).

In the Mediterranean Sea, *P. oceanica* leaves contain 23–40% of carbon, varying with depth, season and leaf age (Augier and Santimone, 1982; Velimirov, 1987; Duarte, 1990; Alcoverro et al., 1995; Gobert et al., 1995; Mateo et al., Chapter 7). Seasonal and daily variations of soluble carbohydrates, starch, and free amino acids were investigated in detail by Velimirov (1984); Pirc and Wollenweber (1988); Alcoverro et al. (2001b). The carbon fluxes of the beds, resulting essentially from *P. oceanica* primary production, vary according to environmental conditions (depth, hydrodynamic conditions, predation pressure) (Pergent et al., 1997b), among populations (Cebrián and Duarte, 2001) and seasons. Primary production is higher at the shallow edge because of higher bed density. Depth also has a significant influence on the distribution of litter: within the beds export rates are highest at shallower stations where the hydrodynamic forces are greater. Consequently, accumulation rates among sites show high variations (i.e. 19–191 g C m^{-2} $year^{-1}$in Romero et al., 1994; 9–112 g C m^{-2} $year^{-1}$ in Matèo et al., 1997; see also Mateo et al., Chapter 7).

Meiofaunal assemblages (Danovaro et al., 2002) (from 0 to 4 cm in the sediment) constitute a biomass of 1.1 g C m^{-2} (i.e. $4{,}010^3$ tons C for the *P. oceanica* meadows of the Mediterranean Sea) with a mean production of 10.0 ± 1.9 g C m^{-2} $year^{-1}$ (i.e. 409×10^3 tons C $year^{-1}$). The seasonal change in meiofaunal production, like benthic bacterial activity (Lopez et al., 1995), seems to be related with the bio-availability of sediment organic matter (Danovaro et al., 2002).

B. Nitrogen and Phosphorus

In both the Mediterranean and southern Australia, environments are characterized by microtidal regimes and relatively low-nutrient environments. Thus, paradoxically *Posidonia* species colonize one of the most nutrient-poor environments in the world (e.g. Copin-Montégut, 1996; Walker, 2000). *P. oceanica* can even colonize ultra-oligotrophic habitats in the Eastern Mediterranean (if this status is defined by the nutrient concentrations and not by the biomass). The nitrogen content in *Posidonia* species varies seasonally and between species and organs (Augier et al., 1982; Duarte, 1990; Gacia et al., 2002). Nitrogen dynamics in Australian *Posidonia* species have been reported for Cockburn Sound, Shark Bay, and Geographe Bay (Hocking et al., 1980; Walker and McComb, 1988; MacMahon and Walker, 1998; Cambridge, 1996; Cambridge and Hocking, 1997; Paling and McComb, 2000).

Contrary to other Mediterranean species such as *Cymodocea nodosa* (Pèrez and Romero, 1994), *P. oceanica* dynamics are not (or little) limited by nutrient availability (e.g. Alcoverro et al., 1995, 1997a) and *P. oceanica* seems better adapted to nutrient-poor conditions relative to smaller Mediterranean seagrasses (Marbà et al., 1996), both from morphological and growth characteristics (Marbà et al., 1996). *P. oceanica* sediments receive enough nitrogen from depostion of decaying leaves to sustain the plants' needs, if recycling is efficient (Gacia et al., 2002). Phosphorus appeared to limit seagrass production in Shark Bay (Australia) (Smith and Atkinson, 1983). If limitation by nutrient availability occurs, the consequences for growth are most obvious during summer (Alcoverro et al., 1997b; Wolterding and Larkum, 2002). Even in oligotrophic areas, such as NW Corsica, fertilizers have little effect on the annual dynamics of *P. oceanica* (Gobert, unpublished data). *P. oceanica* may have developed diverse strategies to buffer and reduce the impact of environmental conditions.

As in many other temperate species, *P. oceanica* has a periodic loss of nutrients due to a seasonal leaf fall (e.g. Hemminga et al., 1991). However, nutrient acquisition (Lepoint et al., 2002a; Lepoint et al., 2004a), storage and remobilization (Alcoverro et al., 2000; Invers et al., 2002), photosynthate translocation (Manzanera and Romero, 2000; Marbà et al., 2002), and nutrient resorption and recycling (Alcoverro et al., 2000; Lepoint et al., 2002b; Lepoint et al., 2003; Lepoint et al, 2004b) all contribute to strategies used by *Posidonia*. On an annual average, 5–50% of the total nitrogen assimilation occurs in roots and 50–79% in leaves (Invers et al., 2002; Lepoint et al., 2002a). In addition rhizomes contribute to the total shoot nitrogen assimilation by 32–54% between autumn and spring (Invers et al., 2002). Below-ground organs appear as a key factor in the nitrogen economy of the plant. Roots and rhizomes are sites for nitrogen assimilation but also as organs for N storage both inorganic and organic (Invers et al., 2002; Lepoint et al., 2003). The leaves, comprising the adult leaves which have little metabolic demand, participate in nitrogen uptake. Adult leaves quickly transfer incorporated nitrogen to growing tissues or storage organs (rhizomes or young leaves) (Lepoint et al., 2002b). Like other marine phanerogams, *P. oceanica* plants are able to take up inorganic nitrogen as nitrate or ammonium (Touchette and Burkholder, 2000a; Romero et al., Chapter 9), even at very low concentrations in the water (i.e. 0.05 μM) (Lepoint et al., 2002b). Incorporation is not limited to periods when nutrient concentrations are high in the environment (i.e. winter, early spring) but occurs year-round. Nitrate and ammonium uptake appear equally important on an annual scale

(Lepoint et al., 2002b). Nitrate is only an important source of nitrogen during winter and early spring, a period of intense incorporation (Alcoverro et al., 2000).

Nutrients incorporated during periods of low growth (but high nutrient availability) (i.e. winter) are stored in rhizomes and new leaves (Alcoverro et al., 2000; Invers et al., 2002). Nitrogen concentrations in leaves are at a maximum in winter. These nutrients can be remobilized and translocated to growing tissues during high growth period (i.e. spring), explaining the decrease of nitrogen concentrations (Alcoverro et al., 2000). Invers et al. (2002) showed that this storage is mainly in an organic form (free amino acids) providing 33% of the nitrogen requirements for spring growth.

In addition to the uptake from external medium, annual nitrogen demand is partially satisfied by resorption of nitrogen from adult leaves and recycling of this nitrogen to ensure the growth of young leaves completes nutrient supply, contributing up to 40% of the annual N needs of the plant (Alcoverro et al., 2000; Lepoint et al., 2002a). Furthermore, contributions from epiphytes (Borowitzka et al., Chapter 19), other seston (Romero et al., Chapter 9) and benthic macro- and microalgae (Mateo et al., Chapter 7), together with the cycling of nutrients from decaying leaves (Gacia et al., 2002) have to be taken into account in both nitrogen and phosphorus supply.

Marbà et al. (2002) showed that strong physiological integrations occur between clonal ramets in some years. This integration allows the transfer of photosynthates and amino acids along rhizomes over a distance of 20–30 cm. This translocation is mainly directed from parent ramets to young and growing ramets. This mechanism could be very important to ensure the N needs and expansion of young ramets which are generally unrooted during the first months of their growth.

In some areas, very low-nitrogen concentrations occur both in the water column and pore water but *P. oceanica* meadows display high biomass and productivity (e.g. Calvi, Corsica). During the summer when the leaves are long (60 cm), the *canopy water* (the water in between shoots) displays both cooler temperatures and much higher nutrient content than the upper water column. The fluxes measured from the sediment to the canopy water are sufficient to provide 20% of the mean daily nitrogen requirements of the *P. oceanica* shoots (Gobert et al., 2002).

VIII. Food Webs

Posidonia beds form extensive habitat for associated fauna and flora, both in the Mediterranean and in southern Australia. Food webs in coastal waters are affected by their presence both, by modifying the ecosystem structure, providing habitat, as well as producing organic matter. This production is then transferred directly through the consumption of leaf material by grazers or indirectly through dissolved organic matter and nutrients leaching from seagrasses being utilized by detritivores or epiphytic algae (Mateo et al., Chapter 7).

Assimilation of *Posidonia*-derived organic matter into food webs occurs not only in the bed, but because of drift of leaf detritus, within habitats that may be located at considerable distances from the bed (see Mateo et al., Chapter 7). Depending on waves and currents, and tidal action in Australia, debris can be deposited within the seagrass bed or exported inshore to the swashzone or beaches, to inshore basins or to the deep oceanic floor (Walker et al., 2001). The presence of *Posidonia* can greatly alter food webs even in the absence of large vertebrate grazers through the provision of substrata for epiphytic alga such as diatoms and filamentous algae or through the production of detritus (Jernakoff and Nielsen, 1997; Jernakoff and Nielsen, 1998). The epiphytic community of *Posidonia* leaves shows a clear depth zonation and daily (Sanchez-Jerez, 1999) or seasonal variation (Mazzella et al., 1989; Russo et al., 2002) and exhibits a time-sequence of leaf colonization (Mazzella et al., 1992; Trautman and Borowitzka, 1999; Lavery and Vanderklift, 2002).

The importance of *Posidonia* to food webs depends largely on the overall productivity of the system. Thus at exposed, low-nutrient sites where primary productivity is low, the presence of seagrass will greatly increase invertebrate and fish production and alter food webs in comparison to unvegetated areas (Edgar and Shaw, 1995c). This is also the case in deep basins and the swash zone where seagrass debris accumulates (Lenanton et al., 1982). In contrast, food webs in nutrient-rich estuaries with dense phytoplankton populations and considerable allochthonous inputs of organic matter may be little affected by the presence of seagrasses. How far and how much *Posidonia* production influences faunal production has not been well quantified.

Posidonia food webs are generally in areas lacking large vertebrate grazers and appear to be fueled primarily by epiphytic production. This situation contrasts with pelagic food webs, which are primarily fueled by phytoplankton, and those occurring below the euphotic zone, which are primarily fueled by detritus. No consensus exists about the most important primary producers in shallow unvegetated habitats, although *Posidonia* and associated epiphyte detritus are probably both major contributors to food webs and locally enhance invertebrate and fish production, including at locations away from the beds where the production occurred.

Direct grazing of *Posidonia* is relatively unimportant in temperate Australian waters, as evidenced by considerable empirical data, with the large number of dietary studies of fishes and invertebrates in temperate beds consistently indicating an extremely low proportion of species that directly consume *Posidonia* material (Klumpp et al., 1989). The only temperate Australian fishes known to ingest large quantities of seagrass are the garfish *Hyporhamphus melanochir* and the leatherjackets *Meuschenia freycineti*, *Monacanthus chinensis*, *Meuschenia trachylepis*, and *Acanthaluteres spilomelanurus* (Bell et al., 1978a,b, 1987; Robertson and Klumpp, 1983; Edgar and Shaw, 1995b), while the crab *Nectocarcinus integrifrons* is also a *Posidonia* grazer (Klumpp and Nichols, 1983; Edgar, 1996).

Seagrass beds can also affect ecosystems through the filtration capacity of filter-feeding invertebrates attached to seagrass leaves. Sponges, ascidians, hydroids, and other filter-feeders remove particles from the water column, and then consolidate the particles and eventually deposit them on the seabed in the form of feces, pseudofeces, and animal bodies. In Cockburn Sound and Marmion Lagoon (WA), the two areas in Australia where estimates have been made on total filtration capacity of *Posidonia*-associated animals, invertebrates were estimated to filter the water column in some seagrass habitats over periods of less than 1 day (Lemmens et al., 1996; Edgar, unpublished data). Whether these estimates are typical or anomalous it remains to be assessed.

Available evidence supports the nursery bed hypothesis for the New South Wales coast, where luderick, bream, and snapper associate as juveniles with seagrass habitat in estuaries (Gray, 1991a,b; Gray et al., 1996). The meagre empirical data available on temperate coasts by Edgar and Shaw (1995a,b,c), however, do not support the hypothesis for other sections of the Australian coast (Jenkins et al., 1997), with the possible exception of juvenile baldchin groper associating with coastal seagrass beds along the central Western Australian coast (Howard et al., 1989). Systematic surveys are urgently required to assess the validity of these hypotheses at a national scale. Surveys are also required to determine whether the primary response of juveniles of the important commercial species in New South Wales is to estuaries or to seagrass habitat within the estuaries.

In the Mediterranean Sea, *P. oceanica*, notwithstanding its important biomass, appears to be a minor food source (Dauby, 1989), but supports high herbivore production due to its large primary production (Cebrian et al., 1996). The low utilization of the enormous carbon reservoir constituted by *Posidonia* leaves can be explained by high C/N ratio, their hard consistency, coupled with a high encrusting rate by calcareous epiphytes, making leaves difficult to assimilate by grazers (Havelange et al., 1997; Dumay et al., 2002). Furthermore, *P. oceanica* contains phenolic compounds (Agostini et al., 1998; Ferrat, 2001) able to discourage grazing as well as a large amount of structural carbohydrates (Buia et al., 2000). In *P. oceanica* meadows, no marine mammals graze but some large marine herbivores (e.g. turtles) spend a large amount of time (90%) at shallow depth in the vicinity of the meadow and ingest seagrass (Hays et al., 2002).

Many grazing studies have been conducted in *P. oceanica* meadows, investigating temporal (day to season) and spatial (small: meters and large: 100 km) patterns (Mazzella et al., 1992; Cebrián et al., 1996; Sanchez-Jerez et al., 1999). Besides *Posidonia*, other plant sources are available for animals, e.g. benthic micro- and macroalgae (on sediment or on rhizomes), epiphytes, and phytoplankton. It seems that epiphyte biomass is partly controlled by the herbivores (Alcoverro et al., 1997a).

Potential consumers of *P. oceanica* leaves are the sparid fish *Sarpa salpa* (Velimirov, 1984), the echinoid *Paracentrotus lividus* (Zupo and Fresi, 1984), the isopod *Idotea baltica* (Lorenti and Fresi, 1983), the polychaete *Platynereis dumerilli* (Mazzella et al., 1995), and even the green turtle *Chelonia mydas* in the eastern basin (Hays et al., 2002). The importance of these macroconsumers shows a great variation from one bed to another along the Mediterranean Coast (i.e. Cebrian et al., 1996). Generally, the authors assumed that these herbivores are a minor factor in the control of *P. oceanica* since grazing accounts only for a small percentage of leaf production (2–15% of the leaf production: Velimirov, 1984; Cebrian et al., 1996; Havelange et al., 1997; Pergent et al., 1997b; Alcoverro et al., 1997a; Cebrian and Duarte, 2001). Polychaetes, isopods, amphipods, decapods, and molluscs, are important links between the primary producers and the final consumers, as they transfer most energy from algal epiphytes and transform significant amount of leaf detritus (Buia et al., 2000). The *Posidonia* system is less efficient than other seagrass ecosystems (e.g. *Zostera noltii*, *Cymodocea nodosa*) in channeling primary production to higher trophic levels (Danovaro et al., 2002).

Isopods directly consume living leaf tissue in Australian species of *Posidonia* (Brearley and Walker, 1995, 1996). In *P. oceanica* beds, Gambi et al. (1997) and Guidetti et al. (1997) described polychaetes boring dead tissue in the remains of leaf bases persisting along rhizomes but also they attack live leaves and removed a small percentage (1–4%) of the sheath production (Guidetti, 2000). In some areas, polychaetes graze 17–41% of the scale biomass and so have strong ecological implications in enhancing scale fragmentation and decay by microbial activity (Gambi, 2000).

The role of *Posidonia* detritus in coastal food webs remains little studied, with few investigations conducted in southeastern or southern Australia on the fate of seagrass or macroalgal debris. The importance of seagrass debris presumably lies primarily in chemical leachates being utilized by bacteria, fungi, microalgae, and protozoa, and by the increasing proliferation of microbes on detrital particles as fragmentation occurs, rather than on the direct ingestion of seagrass material (Fenchel and Harrison, 1976; Fenchel, 1977; Mateo et al., Chapter 7). More protein has been found in surficial microbes than in the decaying seagrass debris with which they are associated (Zimmerman et al., 1979).

In the Mediterranean Sea, decaying *P. oceanica* leaves, with a low proportion of rhizomes, sheaths and seaweed, form the 'debris' (Velimirov et al., 1981). A fraction of dead leaf material enters the food web, depending on the quantity of material exported inshore or offshore (10–95%) (Romero et al., 1994; Matèo et al., 1997; Pergent et al., 1997b; Gacia et al., 2002). As described by Walker et al. (2001), the terminology in seagrass literature can cause confusion, the following different terms should be used: wrack, for transported recognizable leaves; litter, for fragmented material; broken down dead roots, rhizomes, hard to recognize leaves (<0.5 mm) are detritus. *P. oceanica* does not support all consumer nutrition and the microbial growth on leaf material seems to be the major source of nutrition for macroconsumers.

About 50 species of fish are encountered in *P. oceanica* beds, classified as resident (56%), as transient (22%), or as occasional species (22%). The most important families were Labridae, Scorpenidae, Serranidae, and Centracanthidae which account for 41% of the number of species and 87% of the total biomass (Harmelin-Vivien, 1982, 1989).

Studies on the food web structure in *Posidonia* beds (by the direct observation of dietary linkages through gut content analysis or by indirect analysis dietary tracers: lipids and other biochemical markers (Klumpp and Van der Valk, 1984) and radioisotopes have not been conducted systematically in a range of marine habitats around Australia, so the overall contribution of seagrass, seagrass detritus, and seagrass epiphytes, relative to other sources of organic matter, to coastal food webs remains unknown. In Australia, very few attempts have been made to quantify the transfer of *Posidonia* production into coastal food webs (sensu Robertson, 1984), or to determine the relative importance of *Posidonia* production compared to primary production generated by other major plant groups (phytoplankton, macroalgae, benthic microalgae, mangroves).

In the Mediterranean Sea, the relative importance of the different sources in the diet of the main consumers in *P. oceanica* meadows have been approached by the analysis of carbon and nitrogen stable isotopes and by determination of gut contents (Dauby, 1989, 1995; Dauby et al., 1995; Havelange et al., 1997; Jennings et al., 1997; Lepoint et al., 2000; Pinnegar and Polunin, 2000; Vizzini et al., 2002; Mateo et al., Chapter 7). Plankton and seaweed (including epiphytes) constitute the main fraction of the diet of primary consumers (herbivores, suspension- and detritus feeders). Stable isotopes demonstrate that direct seagrass grazers assimilate a non-negligible amount of ingested seagrass carbon: about 20% for *Sarpa salpa* (Havelange et al., 1997). The carbon fraction originating from seagrasses appears extremely low and only dominates in the diet of very few species, e.g. psammivorous holothurians.

Grazers are rarely exclusively plant consumers (e.g. Mazzella and Russo, 1989). For example, the crustacean *Achaeus cranchii* grazes algae on *P.*

oceanica leaves but also eats the associated fauna (Boudouresque and Meinesz, 1982). The herbivore production in *P. oceanica* meadows is much lower than in tropical seagrass meadows, probably due to the higher consumption rates and assimilation efficiencies in tropical seagrass systems (Cebrián et al., 1996).

P. oceanica rhizomes represent a suitable habitat for sciaphilous subtidal phytocoenoses (Panayotidis, 1980), such as epiphytic bryozoans which are qualitatively richer on the rhizomes than on leaves (Kocak et al., 2002). About 70 species of macroalgae grow on rhizome (Piazzi et al., 2002). This plant part is a support providing food and habitat for the associated fauna.

In summary, where it occurs, *Posidonia* plays a major role in shallow water diversity. Some *Posidonia* ecosystems are important as nursery areas but others are less important or have not been studied. While direct grazing of the leaves appears unimportant, food webs based on grazing of the epiphytes growing on *Posidonia* leaves are a major contributor to higher trophic levels. Below-ground detritus-based food webs appear to be less important. There is evidence for wide spatial variation in trophic relations, which is probably linked to local environmental characteristics. Future studies of food web will require innovative use of techniques such stable isotope analyses, as well as further improvements in knowledge of systematics and ecology.

IX. Species Status and Anthropogenic Impact

Despite the ecological and economical importance of seagrass beds, an increasing number of reports document the ongoing loss or regression of seagrasses in all countries (Duarte et al., 2002; Walker et al., Chapter 23; Kenworthy et al., Chapter 25). The surface area occupied by *Posidonia* beds is limited by environmental factors (light, turbidity, salinity, temperature), but in some coastal regions where anthropogenic pressures (trawling, aquaculture, wastewater outfalls) are high, severe damage is observed. The loss of *Posidonia* beds is unfortunately not recent; it has been reported since 1930s (Boudouresque and Meinesz, 1982; Cambridge and McComb, 1984; Shepherd et al., 1989; Larkum and West, 1990; Walker and McComb, 1991). Recent mapping of the historical evolution of *Posidonia* distributions generally shows a decline in seagrass coverage (e.g. Pasqualini et al., 2000; Kendrick et al., 2002) reflecting anthropic activities, port developments, grazer impacts, shading of seagrass leaves by excessive growth of epiphytic algae or phytoplankton following nutrient enrichment of column water (Cambridge et al., 1986; Walker and McComb, 1992; Short and Wyllie-Echeverria, 1996; Chisholm et al., 1997). Climate change will affect seagrass distributions (Short and Neckles, 1999; Duarte et al., in press). The recolonization of altered sites is rare but does occur (e.g. Kendrick et al., 1999, 2000; Meehan and West, 2000; Pergent-Martini and Pasqualini, 2000; Cambridge et al., 2002)—but is slow because *Posidonia* are long lived species with a slow rhizome spread (0.3–21 cm year^{-1}) (Boudouresque et al., 1984; Meinesz and Lefèvre, 1984; Kirkman and Kuo, 1990; Marbà and Duarte, 1998; Marbà and Walker, 1999; Paling and McComb, 2000). The loss of Western Australian *Posidonia* meadows is caused by a reduction in light reaching the meadows, either through decreased water clarity or shading by epiphytic or unattached algae (Cambridge et al., 1986; Walker and McComb, 1992; Kendrick et al., 2002; Walker et al., Chapter 23). Some mechanical transplantation of *Posidonia* species has been conducted with some success (Paling et al., 2001).

The main strategies for marine environmental management in Australia (7.7 × 10^6 km^2 and 18 millions permanent residents) include maintenance of water quality, prohibiting or regulating destructive and unsustainable activities, zoning for particular uses to separate and control incompatible uses, protection of vulnerable and threatened species and regulation of fisheries through licenses, size limits, quotas, etc. Australia is a world leader in using Marine Protected Areas (Fogarty et al., 2000; Kenworthy et al., Chapter 25) but our understanding of the marine environment is still patchy.

The Mediterranean Sea (3 × 10^6 km^2 and 44 million permanent residents) is known for the considerable diversity of its fauna and flora as well as for the high rate of species endemism. But generally, Mediterranean countries have coastlines that are the most intensively used in the world for tourism and related recreational activities. The coastline (including islands) receives some one hundred million visitors per year from all nationalities. As such, the Mediterranean coast and nearshore waters experience the increasing impact of tourism but also the effects of resident demographic growth. In addition, the coastal region supports agriculture and mariculture as well as wild fisheries, industry, and navigation.

Monitoring strategies have been recently proposed to control and conserve meadow habitats (e.g. Moreno et al., 2001). Seagrass meadows are a priority habitat under the European Union Species and Habitats Directive (H&SD, 92/43/EEC).

The protection and conservation is of primary importance, but the replanting of *Posidonia* shoots is slow and difficult. Survival of transplants is low in the Mediterranean (Molenaar and Meinesz, 1995; Molenaar et al., 2000), and only about 40% survive in southern Australia (Lord et al., 1999). Transplantation is accompanied by modifications of biometry, and modifications of C, N, and P content, which reflect weakness of the strategy (Lepoint et al., 2004a). One year after transplanting, shoots are still unable to satisfy their nutrient demand (Gobert, 2004; Lepoint et al., 2004; Vangeluwe et al., 2004).

The introduction of exotic marine organisms, from accidental release, vessel ballast water, hull fouling, and aquaculture, remains an area of concern (Boudouresque and Verlaque, 2002; Duarte et al. in press; Ralph et al. Chapter 24), particularly where the introduced species are competitors for soft bottom substratum such as the algae *Caulerpa taxifolia*, and *Caulerpa racemosa* in the Mediterranean (Meinesz et al., 1993; Deville and Verlaque, 1995; Ceccherelli and Cinelli, 1999) and the fan worm *Sabella spallanzanii* in southern Australia (Lemmens et al., 1996).

Aquaculture of fish and algal biomass has been shown to produce major environmental impacts, particularly due to shading, eutrophication, and sediment deterioration through excess organic inputs (Seymour and Bergheim, 1991; Shireman and Cichra, 1994; Dosdat et al., 1995; Holmer et al., 2001). The effects of fish farms and other aquaculture developments are of concern as areas of productive seagrass habitats are often targeted for such developments, such as in the Mediterranean coast (Delgado et al., 1999; Pergent et al., 1999). Fish pens have been demonstrated to cause seagrass loss (Delgado et al., 1999; Pergent et al., 1999). Extensive and intensive aquaculture developments are expanding worldwide, increasing the risk of more loss.

X. Summary

The nine species of *Posidonia* occur in two separate biogeographic regions: the Mediterranean Sea and the temperate southern coasts of Australia. Probably separated during the Late Eocene, Mediterranean and Australian species of *Posidonia* show large divergences in the DNA sequences and in shoot phenology and growth characteristics. They are all perennial plants, with linear leaves attached to a leaf-sheath which remains underground after the leaf-blade has been shed. The genus consists of large seagrasses with long leaves, and low rates of leaf and shoot turnover compared to smaller, fast growing seagrasses. They are monoecious, and have hermaphrodite inflorescences without a perianth. They inhabit exposed to moderately sheltered areas, in nutrient-poor waters with low tidal ranges. They colonize a great range of depths (0–45 m) and can settle on fine sand to rocky substrate. Species of *Posidonia* have high biomasses, with distinct seasonal variations in productivity and are influenced by light, temperature, nutrients, and water movement. Despite their high biomass, species of *Posidonia* appear to be a minor food source, as direct grazing is relatively unimportant but the presence of *Posidonia* can greatly alter species diversity and food webs by the provision of substrata for other organisms to settle and grow on.

Posidonia meadows are regressing in many regions as a direct result of anthropogenic activities. Pollution and nutrient enrichment have been linked to impacts such as overgrazing, shading of seagrass leaves by excessive growth of epiphytic algae or phytoplankton. Deleterious effects are often difficult to detect in time: the health status of the interconnected *Posidonia* shoots, generally expressed in terms of biomass and production, does not directly reflect the environmental degradation, and by the time *Posidonia* is showing signs of regression, the rest of the ecosystem is already largely affected. The transplantation of these long-live species is slow and costly, and it is wiser to ensure their preservation by protection, rather than by the difficult process of ecosystem restoration.

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Chapter 18

The Biology of *Thalassia*: Paradigms and Recent Advances in Research

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I. Introduction

A. The Genus Thalassia

The two species belonging to the genus *Thalassia* (Family: Hydrocharitaceae), *T. testudinum* Banks ex König and *T. hemprichii* (Ehrenberg) Ascherson are widely distributed in shallow coastal areas in the tropics and subtropics of the Western Atlantic and Indo-Pacific, respectively (den Hartog, 1970; Phillips and Meñez, 1988; Spalding et al., 2003), and they are considered to be 'twin species'. The current hypothesis, based on paleographical data, is that they derived from a common ancestor in the Tethys Sea, until continental drift separated the modern West Pacific and West Atlantic (before the Miocene, >24 million years ago). Lumbert et al. (1984) reported a fossil leaf of *Thalassia* in the Avon Park Formation, Florida from the late Middle Eocene, which was identical to leaves of present-day *Thalassia*. Both species are very similar morphologically, and on a macro-scale, they can only be separated on the basis of counts and dimensions of the styles and stamens of the flowers (see section VI.B). However, genetically, the two species show divergence, as was shown by McMillan (1980) using allozymes, and very recently by Waycott and Les (2000) using chloroplast ribosomal (trnL) DNA loci and nuclear ITS sequences.

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Considering the habitat types where the two species of *Thalassia* occur, their beds could potentially extend over huge areas (hundreds of thousands of square km). However, no serious attempts at mapping their total surface area have been undertaken. Even without detailed knowledge of their exact distribution and abundance, both species are known to play an enormous role in the ecological equilibrium of many tropical coasts. *Thalassia*-dominated-beds can either be found in marine lagoons or coastal estuaries, which are often fringed by mangroves or coral reefs, and it is very likely that narrow interactions exist between seagrass, coral reef, and mangrove systems. These interactions include modification of hydrodynamic environment (the reefs provide low wave-energy environments necessary for the establishment of seagrasses and mangroves, and the seagrasses reduce water motion on a smaller scale which allows stabilization of sediments), sediment production (by the reef organisms and calcareous algae associated with the seagrasses), export of organic material (mainly by seagrasses and mangroves toward the reef), and migratory movements of fauna between the three systems (Ogden and Gladfelter, 1983; Bosence, 1989; Hemminga et al., 1994; Holmer et al., 1999; Nagelkerken et al., 2000). *Thalassia* has the potential to attain high biomass and production rates, and Duarte and Chiscano (1999) who compiled data from many sites, reported an average aboveground biomass of 519 and 87 g dry mass m^{-2} for *T. testudinum* and *T. hemprichii*, respectively. The differences in mean aboveground biomass between the two species are most likely not due to differences in the plant body but caused by differences in the environmental settings and co-occurring seagrass and macroalgae species in the Atlantic and Indo-Pacific (see also Section VIII). These two species have the best developed root and rhizome system of all seagrass species in the western Atlantic, which is better developed than most other grasses in the Indo-Pacific. Belowground biomass (which includes all tissues except for the leaves) accounts for ~80–92% of the total biomass (Brouns, 1985; van Tussenbroek, 1996; Kaldy and Dunton, 2000). Duarte and Chiscano (1999) reported mean aboveground production rates of 5.0 and 3.7 g dry mass m^{-2} day^{-1} for *T. testudinum* and *T. hemprichii*, respectively; belowground tissues (excluding roots) only contribute between 5 and 27% (generally varying between 10 and 20%) of the total production for this genus (Brouns, 1985; Gallegos et al., 1993; Vermaat et al., 1995; van Tussenbroek, 1996), but Kaldy and Dunton (2000) reported an exceptionally high contribution of 35% by rhizomes in the total plant production for *T. testudinum* in Laguna Madre. Although *Thalassia* is often the dominant primary producer in tropical coastal seagrass communities, other macrophytes (seagrasses and macroalgae), benthic and epiphytic diatoms and phytoplankton also contribute, to a greater or lesser degree, to the total community production, and *Thalassia*-dominated meadows are amongst the most highly productive marine systems on Earth (Westlake, 1963; Erftemeijer, 1993; Duarte and Chiscano, 1999).

II. Basic Environmental Requirements

Thalassia is a genus of the tropics and subtropics: *T. testudinum* occurs between 9°S and 32°N, and the distribution range *T. hemprichii* falls between 28°S and 32°N (Spalding et al., 2003). Thus, its global distribution is largely determined by incoming irradiation and related temperature. Regional distributions are considerably more complex, with temperature, salinity, light attenuation, sediment composition, and sediment depth playing major roles.

Seagrasses from tropical environments generally have reduced temperature tolerances compared with temperate-zone counterparts. Their range of temperature tolerance is only half that of organisms from temperate waters (Moore, 1963), which is due to loss of resistance to cold environments, whereas their upper thermal limit is generally not much greater than that of organisms from warm-temperate regions (Zieman, 1975a). *Thalassia* can neither tolerate prolonged exposure to high temperatures nor long-term desiccation on intertidal flats (Brouns, 1985; Stapel et al., 1997). Phillips (1960) found that *T. testudinum* preferred temperatures of 20–30°C in South Florida, and the optimum temperature range for growth for this species is between 23 and 31°C (Barber and Behrens, 1985). This species tolerates short-term exposure to high temperatures (33–35°C) but growth rapidly falls off when these temperatures are sustained (Zieman, 1975a). In Puerto Rico, Glynn (1968) found that temperatures of 35–40°C killed the leaves of *T. testudinum* on a tidal flat, but that the rhizomes of the plants were apparently unaffected. On shallow vegetated banks, temperatures rise rapidly during spring low tides, and the high temperatures, coupled with desiccation, kill vast quantities of leaves that are later sloughed off. This defoliation process occurs sporadically throughout the year and seems to pose no long-term problem for the plants. Brouns (1985) reported similar negative effects of desiccation at extreme low tides for monospecific *T. hemprichii* meadows in Papua New Guinea. In the subtropical waters of Texas and Florida, the most severe mortality of *T. testudinum* is usually caused by severe cold rather than heat, even though these seagrasses from the extreme northern distribution range showed a greater tolerance to chilling temperatures (at 2°C, during 4–12 h), than their southern counterparts (McMillan, 1979).

The optimum salinity range for *T. testudinum* has been reported to be from 24 to 35 psu (Phillips, 1960; McMillan and Moseley, 1967; Zieman, 1975a), but *Thalassia* tolerated a broad salinity range for very brief exposures, ranging from 3.5 to 5.0 psu (den Hartog, 1957 in Sculthorpe 1967) to 60 psu (McMillan and Moseley, 1967), although such exposures commonly result in leaf loss. Following the passage of hurricane Donna in South Florida in 1960, Thomas et al. (1961) considered the damage to *T. testudinum* by fresh water runoff to have been more severe than the physical effects of the high winds and water surge. Heavy freshwater releases reported in South Florida (Thomas et al., 1961) and Venezuela (Pérez and Galindo, 2000) caused mortality of macro algae as well as vertebrate and invertebrate fauna associated with seagrass meadows, but although *T. testudinum* was heavily defoliated, the buried rhizomes remained intact, and leaf recovery was rapid.

T. testudinum requires a minimum sediment depth of ~25–50 cm to achieve lush growth (Zieman, 1975b), although meadow formation occurs at lesser sediment depths (Scoffin, 1970). Sediment composition and the proportion of finer-grained particles vary as a function of leaf density of *T. testudinum*. In the Bahamas, bare sediments had only 1–3% fine-grained material, while dense *T. testudinum* had more than 15% of fine-grained sands (Scoffin, 1970). Similarly, dense *T. testudinum* meadows raise the elevation within the meadows due to sedimentation (Ginsburg and Lowenstam, 1958; Zieman, 1975b; Durako and Moffler, 1985c), and increase the concentration of sedimentary organic matter (Wood et al., 1969) resulting in higher protein levels in rhizomes of *T. testudinum* from the middle of the beds (Durako and Moffler, 1985c).

T. testudinum may be found as deep as 10 m in clear water (Phillips and Meñez, 1988), but is confined to maximum depths of 1–2 m in turbid habitats (Phillips, 1960; Zieman, 1982). For seagrasses in general, lower depth limits are set by ambient light levels (Dennison and Alberte, 1985), as the photosynthates produced in the leaves in light, are transported to subterranean tissues, where they are invested in new shoot growth (an investment on top of carbohydrate storage and respiration). Lee and Dunton (1996) reported that *T. testudinum* in Laguna Madre (Texas, USA), required an annual quantum flux in excess of 1628 mol m^{-2} in order to maintain a positive carbon balance, which corresponded with 14% of the surface irradiance.

III. Historical Development in Research

Few areas of marine or environmental science have seen an explosion of research and literature to match that produced by studies of seagrasses in the past three to four decades. Early work with *Thalassia* focused principally on taxonomy, anatomy, distribution, and limited autecology (Phillips, 1960; Tomlinson and Vargo, 1966; Tomlinson, 1969a,b, 1972, 1974; den Hartog, 1970). Most early studies were limited to sites where the scientists could wade at low tide, and deeper samples were restricted to random and disruptive ship-borne dredges and cores. This changed dramatically and rapidly in the mid-1960s with the emergence of reliable and simpler SCUBA, which enabled the scientist to dive throughout the entire depth range of *Thalassia* and other seagrasses, and to spend considerable time in situ. In a study on the marking method of estimating production of *T. testudinum*, Zieman (1974) cited 16 references. Less than 10 years later, a synthesis of seagrass studies in South Florida (Zieman, 1982), where *T. testudinum* is the dominant species, contained 529 references, of which ~40% concerned (directly or indirectly) *T. testudinum* communities. Of these, 33 were from prior to 1960, 119 were from 1960 to 1969, and 377 were post 1970, showing the rapid increase in studies of seagrass ecosystems during this time. While field instrumentation underwent tremendous changes and development during this period, particularly the size reduction and reduced power demands brought about by integrated solid-state technology, it is impossible to overestimate the importance of allowing the scientist to spend repeatedly extended times on site underwater. On the other hand, new laboratory instrumentation and techniques, such as stable isotope analysis and molecular genetics, have opened up our view of community dynamics and evolution of the seagrasses. In the present chapter, we will cover several fields of seagrass research, where the genus *Thalassia* has played a substantial role, and in which existing paradigms have been challenged in the light of new approaches and developments.

IV. *Thalassia*–Sediment Interactions

Thalassia, like many other seagrass species, has major effects on the detention and deposition of particles in the water column. The dissipation of wave and current energy by the plant canopies results in increased deposition rates of the particles (see Koch et al., Chapter 8). The intensity of this canopy effect depends on a complex way on leaf morphology, stiffness, and density. The rhizomes and roots, on the other hand, stabilize the sediments and thus prevent resuspension of the particles (see Koch et al., Chapter 8). The combined effect of reduced resuspension and enhanced deposition results in enhanced deposition of particles in *Thalassia* beds (Almasi et al., 1987; Koch, 1999b; Gacia et al., 2003). There is often organic matter associated with these particles, and as a consequence non-seagrass derived organic matter contributes significantly to sediment carbon pools in seagrass beds. The total sediment organic pool in seagrass meadows depends on seagrass litter production, non-seagrass local production (e.g. benthic microalgae), and allochthonous organic matter, in combination with the relative utilization and degradation of these carbon inputs (see Mateo et al., Chapter 7). The relative contribution of *Thalassia* derived organic matter can easily be traced using stable carbon isotope signatures and varies from a small ($<30\%$) contribution (Hemminga et al., 1994) to predominant (Jones et al., 2003).

Thalassia also contributes to the sediment accumulation through calcium carbonate production of the epiphyte community on the leaves (see also Borowitzka et al., Chapter 19). Calcium carbonate production of the epiphytes scales with seagrass production, and that of associated calcified algae such as *Halimeda* spp. Gacia et al. (2003) reported calcium carbonate production rates associated with *T. testudinum* leaves of 0.49–7.7 g $CaCO_3$ m^{-2} day^{-1} in the tropics and 0.08–2.85 g $CaCO_3$ m^{-2} day^{-1}, in the subtropics. For tropical and subtropical *T. hemprichii* epiphyte calcium production rates were 0.92–6.52 and 0.38 g $CaCO_3$ m^{-2} day^{-1}, respectively. Calcium carbonate derived from *Thalassia* epiphytes contributes variable to sediment deposition: from negligible to significant (35%, Gacia et al., 2003). However, dissolution of carbonates, related to carbon dioxide production during aerobic respiration of organic material, has also been reported to occur in seagrass beds. This aerobic respiration is maintained by root oxygen release. Burdige and Zimmerman (2002) reported significant carbonate dissolution in *T. testudinum* beds with rates (4–11 mmol m^{-2} day^{-1}) depending on seagrass bed density. Carbonate dissolution in *T. testudinum* beds is less than carbonate production (5–77 mmol m^{-2} day^{-1}; see above) indicating that on the whole seagrass-derived carbonate accumulates in the sediments.

V. Nutrient Dynamics

Nutrient research in *Thalassia* has mainly been focused on the dissolved inorganic nitrogen and phosphorus (Hemminga and Duarte, 2000a,b), although micronutrients, such as iron may also play an important role, locally, in moderating the productivity of *Thalassia* (Duarte et al., 1995). For a proper understanding of nutrient dynamics, the availability, net uptake and re-use of nutrients by plants should be taken into account, as well as processes of nutrient losses (export of material, denitrification, and foraging fauna), gains in the community (sedimentation, N_2-fixation and water enrichment; Hemminga et al., 1991; Romero et al., Chapter 9) and the interaction with the abiotic compartment (Thomas and Cornelisen, 2003).

A. Nutrient Availability

In the tropical and subtropical shallow coastal areas where *Thalassia* occurs, water-column dissolved inorganic concentrations are generally low ($PO_4^{3-} < 1\mu M$ and $NH_4^+ + NO_3^- < 3\mu M$; Tomasko and Lapointe, 1991; Agawin et al., 1996; Ziegler and Benner, 1999), with exception of areas with high river inflow or which are frequently exposed to the air during low tides (Erftemeijer and Herman, 1994; Stapel et al., 1997). The majority of the N and P pools in *Thalassia* meadows are present in the sediments, adsorbed to sediment particles or bound in organic matter and therefore largely unavailable to the plants (Erftemeijer and Middelburg, 1995; Stapel et al., 1996a; Koch et al., 2001). Jensen et al. (1998), for example, reported that total sediment P in the upper 20 cm in subtropical carbonate sediment in Bermuda was 500-fold larger than the pool of P dissolved in pore waters. Pore-water NH_4^+ concentrations in meadows of both *Thalassia* species usually vary between 2 and 200 μM (Erftemeijer, 1994; Lee and Dunton, 1999b; Table 1). But exceptionally high figures (of up to 800 μM) have been reported in *T. hemprichii* meadows from the East African coast (Erftemeijer and Herman, 1994; Stapel et al., 1996a; Marbà et. al., 2002), and in *T. testudinum* beds in the Laguna madre (Lee and Dunton, 2000). Pore-water PO_4^{3-} concentrations are generally higher in *T. hemprichii* beds (up to 35 μM) compared to *T. testudinum* meadows (<1.5 μM; Fourqurean et al., 1992a; McGlathery et al., 2001). The grain size of the sediments, determining diffusion rates of nutrients, as well as the sediments' origin (terrigenous or marine) and the so far poorly studied biogeochemical interactions, may be an important factor controlling nutrient availability in pore water, as has been put forward by Erftemeijer et al. (1994), Erftemeijer and Middelburg (1995) and Stapel et al. (1996a) for *T. hemprichii*. The pore-water chemistry is also affected by current velocity of the overlaying water column. Under stagnant water conditions, sulfide levels may increase in pore water, while high flow rates may lead to reduced nutrient concentrations (Koch, 1999a). Nutrient concentrations in *Thalassia* beds show annual fluctuations in sediment pore water, in the water column, as well as in the plant material, which are due to seasonal influences (Erftemeijer and Herman, 1994; Lee and Dunton, 1999a,b; Ziegler and Benner, 1999).

The oligotrophic waters in which *Thalassia* proliferates have very low concentrations of dissolved inorganic nutrients, but in these waters, total dissolved nutrient pools (including dissolved organic nitrogen and phosphorus) may be up to five times higher than the total concentration of the dissolved inorganic nutrients (Hansell and Carlson, 2002). The availability of the dissolved organic nutrients to *Thalassia* is not well known and is likely to be variable because it depends on the composition and molecular size of the compounds. Little is known concerning the uptake of organic nutrients by *Thalassia* or any other seagrass (see Romero et al., Chapter 9), but other submerged primary producers such as marine algae and bacteria and various macrophytes are known to assimilate organic nutrients (Lipson and Nasholm, 2001).

B. Nutrient Limitation

Duarte (1990) suggested that seagrass plants with nutrient levels in leaves below the median values for seagrasses of 1.8% N and 0.20% P (as % DW) were nutrient-limited. Leaf N-concentrations of *T. testudinum* and *T. hemprichii* ranged between 0.88–3.96% and 1.5–2.8% of DW, respectively (Fourqurean et al., 1992b; Stapel et al., 1997; Jensen et al., 1998). For P, these values varied between 0.048 and 0.274% of DW for *T. testudinum* and 0.11–0.23% of DW for *T. hemprichii* (Erftemeijer, 1994; Terrados et al., 1999a; Fourqurean and Zieman, 2002). The lower values of tissue N- and P-concentrations of both species are well below the critical levels according to Duarte (1990), but these levels alone cannot be used as indicators of N- or P-limitation in *Thalassia* (see Table 1). Experimental additions of nutrients to the sediment have increased seagrass size or growth, nutrient content, shoot density, and the above- to belowground biomass ratio in the Philippines, occasionally in the Caribbean, but not in Indonesia. Terrados et al. (1999a) found that the N-content in leaves of *T. hemprichii* reflects the availability of N in the sediment. Within the limits of these the limits of these studies, this seems consistent with the values given in Table 1. The existence of N limitation in *T. testudinum* beds probably depends on in situ sediment NH_4^+ concentration, and hence this may also be used as an indicator of the N status for seagrass growth (Lee and Dunton, 2000).

C. Nutrient Uptake by the Plants

Thalassia takes up nutrients from its environment with its leaves and roots. Leaves and roots contribute about equally to the plant's total nutrient acquisition (Erftemeijer and Middelburg, 1995; Lee and Dunton, 1999b). Significant differences in pore-water NH_4^+ concentrations between two sites in the Gulf of Mexico (averages respectively 87 and 26 μM) did not affect the relative contribution of roots and leaves to the total N requirements in *T. testudinum* (Lee and Dunton, 1999b).

The uptake rate of nutrients from the pore water by *Thalassia* roots is largely controlled by sediment parameters and is generally diffusion limited, whereas the uptake of nutrients from the water

Table 1. Sediment nutrient addition experiments in *Thalassia* meadows. The pore water and water column nutrient concentrations are in µM, plant nutrient contents as % DW.; –, not determined; bdl, below detection level. Please note that detection of limitation is not always consistent with plant nutrient contents. See text for more details.

Site	Sediment		Pore water			Water column			Plant leaf		Plant rhizome		Nutrient limited		Reference
	Type	Enrichment	PO_4^{3-}	NH_4^+	NO_3^- NO_2^-	PO_4^{3-}	NH_4^+	NO_3^- NO_2^-	P (%)	N (%)	P (%)	N (%)	P	N	
T. testudinum															
Corpus Christy Bay	Sand 91%	None	–	79.8	–	–	1.16	0.84	–	2.6	–	1.2	–	No	Lee and Dunton (2000)
	Silt 9%														
		N	–	756.2	–	–	1.16	0.84	–	2.7	–	1.3	–		
Laguna Madre	Sand 71%	None	–	31.3	–	–	1.22	0.84	–	1.75	–	0.8	–	Yes	
	Silt 29%	N	–	738.9	–	–	1.22	0.84	–	2.6	–	1.1	–		
T. hemprichii															
Barang Lompo	Coral sand	None	7.5	82.2	3.4	0.8	1.4	0.9	0.17	2.7	0.09	0.5	No	No	Erftemeijer et al. (1994)
		N + P	13	109	3.4	0.8	1.4	0.9	0.12	3.0	0.07	0.7			
Kudingareng Lompo	Coral sand	None	7.3	50.9	–	–	–	–	0.15	2.1	0.09	1.2			
		N + P	~12	–	–	–	–	–	0.19	2.1	0.16	1.1			
Palanro	Terrigenous	None	8.7	23.0	5.2	3.3	bdl	1.5	0.14	1.6	0.12	0.6			
		N + P	~14	–	5.2	3.3	bdl	1.5	0.15	1.7	0.10	0.6			
Silaqui	Coral sand	None	0.9	8.3	1.4	0.2	1.8	0.6	0.22	2.5	0.15	1.1	Yes	Yes	Agawin et al. (1996)
		N + P	55.9	111.3	2.3	0.2	1.8	0.6	0.28	2.9	0.22	2.0			
Lucero	Coral sand	None	0.6	10.2	1.5	0.1	1.7	0.5	0.23	2.7	0.12	1.0			
		N + P	35.7	40.1	1.5	0.1	1.9	0.6	0.30	2.8	0.20	1.8			

column depends more on the uptake capacity of the leaves (Stapel et al., 1996a). Stapel et al. (1996a) determined the maximum uptake rate ($V_{\max}$) and the half-saturation constant (K_m; Michaelis-Menten) of ammonium and phosphate uptake by the leaves of *T. hemprichii* plants from three contrasting locations in Indonesia, but did not find significant differences. Lee and Dunton (1999a) studied the leaf-uptake rates for NH_4^+ in *T. testudinum* in the USA and found much lower values for the uptake characteristics. The $V_{\max}$ for NH_4^+ uptake by *T. testudinum* leaves varied between 7.8 and 17.5 μMol g^{-1} DW h^{-1} (Lee and Dunton, 1999a), whereas that of *T. hemprichii* leaves ranged between 25 and 48 μMol g^{-1} DW h^{-1} (Stapel et al., 1996a). Additionally, K_m for ammonium uptake by leaves of *T. testudinum* and *T. hemprichii* ranged between 3.9 and 23.3 μM and 14–97 μM, respectively (Stapel et al., 1996a; Lee and Dunton, 1999a). These figures indicate that *T. testudinum* leaves have a lower capacity for NH_4^+ uptake, but a higher uptake affinity than *T. hemprichii*, suggesting that *T. testudinum* might be better adapted to growth under low nitrogen conditions. $V_{\max}$ for inorganic phosphate by *T. testudinum* was 1.9–2.1 μMol g^{-1} DW h^{-1} for leaf uptake and 0.38–0.57 μMol g^{-1} DW h^{-1} for uptake by the roots (Gras et al., 2003). Stapel et al. (1996a) reported somewhat higher rates for phosphate uptake by *T. hemprichii*: ∼2.2–3.2 and 1 μMol g^{-1} DW h^{-1} for leaf and root uptake, respectively.

Abiotic parameters that influence the nutrient uptake by leaves are ambient irradiance and water movement. Both current velocity and turbulent energy affect the nutrient uptake by the leaves of *Thalassia* (Thomas et al., 2000; Thomas and Cornelisen, 2003; Koch et al., Chapter 8). An increase in current velocity causes a decrease in the thickness of the diffusion boundary layer and a gain in nutrient uptake by leaves (Koch, 1994). Recent work on meadows of *T. testudinum* indicate that ammonium uptake can even be predicted using empirically derived engineering equations that describe the transport of chemicals between a fluid and a rough surface (Thomas et al., 2000). The influence of ambient irradiance on the uptake of inorganic N and P by *T. testudinum* and epiphytes is less clear. Kraemer and Hanisak (2000) found a significant positive correlation between irradiance and nutrient uptake, whereas Lee and Dunton (1999b) found no difference in nutrient uptake in light or dark.

D. Nutrient Losses and Gains in Thalassia Meadows

The loss of nutrients from a *Thalassia* meadow, like that from other seagrass meadows, occurs primarily through denitrification (Shieh and Yang, 1997), sediment resuspension (Koch, 1999b), the export of *Thalassia* leaves (Zieman et al., 1979) and herbivory (Heck and Valentine, 1995; Valentine and Duffy, Chapter 20). These processes are strongly related to leaf senescence (Hemminga et al., 1991), water flow and turbulence (Koch and Gust, 1999) and herbivore action ('sloppy feeding'; Valentine and Heck, 1999). Fauna can consume up to 25% of the annual leaf production (Klumpp et al., 1993), which is a substantially larger loss than the water flow export of leaf material from *Thalassia* meadows, estimated to be maximally 10% (Greenway, 1976; Stapel et al., 1996b). Nutrients in *Thalassia* seagrass meadows are replenished by the accumulation of sestonic particles in the meadow (Agawin and Duarte, 2002), sedimentation of allochthonous material (Almasi et al., 1987) and nutrient uptake by seagrasses and other primary producers (Wear et al., 1999), especially diatoms (Sterrenburg et al., 1995). These processes are all controlled by water movements (Koch, 1994; Thomas et al., 2003). N_2-fixation, which is positively related to the belowground biomass (Capone and Taylor, 1980), may contribute up to 8% of the N requirement of *Thalassia* (Hemminga et al., 1991; Moriarty and O'Donohue, 1993). Patriquin (1972) argued that essentially all the fixed nitrogen requirements of *T. testudinum* meadow could be supplied by heterotrophic nitrogen fixation within the rhizospheric sediments.

While processes of nutrient loss are relatively well defined, those involved in nutrient gains and retention in *Thalassia* meadows are far less clear. The persistence of often highly productive *Thalassia* beds in oligotrophic environments has therefore been considered as rather paradoxical. In these environments, *Thalassia* should possess efficient nutrient conservation mechanisms, but Hemminga et al. (1999) reported that *T. hemprichii* appeared to be rather wasteful with nutrients, and the low efficiency of utilization of internal nutrient pools seemed to be more characteristic for species of nutrient-rich areas rather than of nutrient-poor habitats. The main strategies for efficient internal nutrient conservation are considered to be a prolonged leaf lifespan (Hemminga et al., 1999) and internal resorption of nutrients from senescent leaves (Nienhuis et al., 1989; Hemminga et al., 1991). The average leaf lifespan for *Thalassia* is ~50 days, which is rather short compared to other (sub) tropical seagrass species, like *Enhalus* and *Syringodium* (~100 and 90 days, respectively; see review by Hemminga et al., 1999). Stapel and Hemminga (1997), furthermore, found for *T. hemprichii* that the maximum potential resorption of nitrogen and phosphorus from senescent leaves was equivalent to 18–28% of the plants' N- and 31% of the plants' P-demand, respectively. Usually, only 56–76% of these maximum values could be realized, because of loss of leaf tissue due to leaf fragmentation and premature detachment. Stapel et al. (2001) reported evidence for efficient external re-use of nutrients via the detrital pathway. The uptake of nutrients by the leaves probably plays a very important role in this process by efficiently recapturing the nutrients that are released in the water column from decomposing *Thalassia* leaves, and thereby contributing to nutrient conservation for the *Thalassia* meadow as a whole. This external re-use of nutrients is closely related to nutrient acquisition via the trapping of seston particles in the meadow and nutrient uptake by epiphytic and epibenthic primary producers. These organic nutrient pools are eventually regenerated in the sediments and the liberated nutrients then become available for root uptake and, after diffusion, for leaf uptake. The capturing and retention of these particulate organic nutrient pools depends on *Thalassia* bed size. Increasing *Thalassia* bed size may therefore also coincide with increasing nutrient retention, which, especially in nutrient-poor environments, may increase chances of survival. The highly dynamic conditions of the marine coastal environment, causing premature loss of leaves and leaf fragments, may have favored the development of an efficient nutrient conservation strategy outside the living plant over internal conservation strategies.

Research into the nutrient dynamics of *T. hemprichii* and *T. testudinum* meadows are, like their geographic distribution, strikingly isolated from each other. For a better understanding of the nutrient dynamics of *Thalassia*, comparative research should be carried out, including studies along the East African coast. Important aspects that are less well understood in the nutrient dynamics of *Thalassia* and that should receive considerable attention are the role of the microbial community in the regeneration of nutrients from *Thalassia* tissue, the role of other primary producers, especially microalgae (diatoms), in fixing nutrients in the system, and the role of microelements, especially iron. The sediment compartment with its complex biogeochemical interactions remains, so far, under investigated, and only recently has received serious attention (Holmer et al., 1999; Terrados et al., 1999b; Enríquez et al., 2001; Holmer et al., 2001). Also, considerably more research is needed to link the sedimentary and nutrient regeneration processes to nutrient absorption by the living seagrass.

VI. Plant Development

A. Vegetative (Clonal) Growth

As with all seagrasses, the vegetative habit of *Thalassia* is clonal and consists of a horizontally creeping rhizome (long shoot) with branches (vertical rhizomes or short-shoots), which bear the foliage-leaves (Figs. 1A and B). But in contrast with the other seagrasses, in *Thalassia,* the distinction between the leaf-bearing vertical rhizomes and the horizontal rhizome is absolute. The following description is mainly based on the studies of Tomlinson on *T. testudinum.* The morphological traits of the vegetative body of *T. hemprichii* seem to be similar to those of *T. testudinum* (Tomlinson, 1974), and no detailed analysis of vegetative development has been realized for the first species to allow comparison. The meristem at the apex of the horizontal rhizome (Figs. 1C and D) forms scale-leaves (or scales), roots and squamules (or intravaginal scales: very small scale-like structures in between the leaves), whereas the meristem at the apex of the vertical rhizome forms foliage-leaves (or leaves), roots, squamules, and flowers (Figs. 1E and F). The root primordia always emerge unilaterally, on the lower side of the horizontal rhizome and either on the left or right site of the vertical rhizomes (Tomlinson and Vargo, 1966; Fig. 1I). Branching is monopodial (Tomlinson and Vargo, 1966), and the apical meristems of the horizontal and vertical rhizomes produce leaf-opposed lateral branches of the opposite kind; that is, horizontal rhizome apical meristems produce vertical rhizomes, and vice versa (Tomlinson and Bailey, 1972; Figs. 1A–C and E). However, in exceptional cases, two foliar groups emerge from the vertical rhizomes ('twin shoots'; Durako, 1995; van Tussenbroek, unpublished data), and Durako (1995) found that up to 40% of the

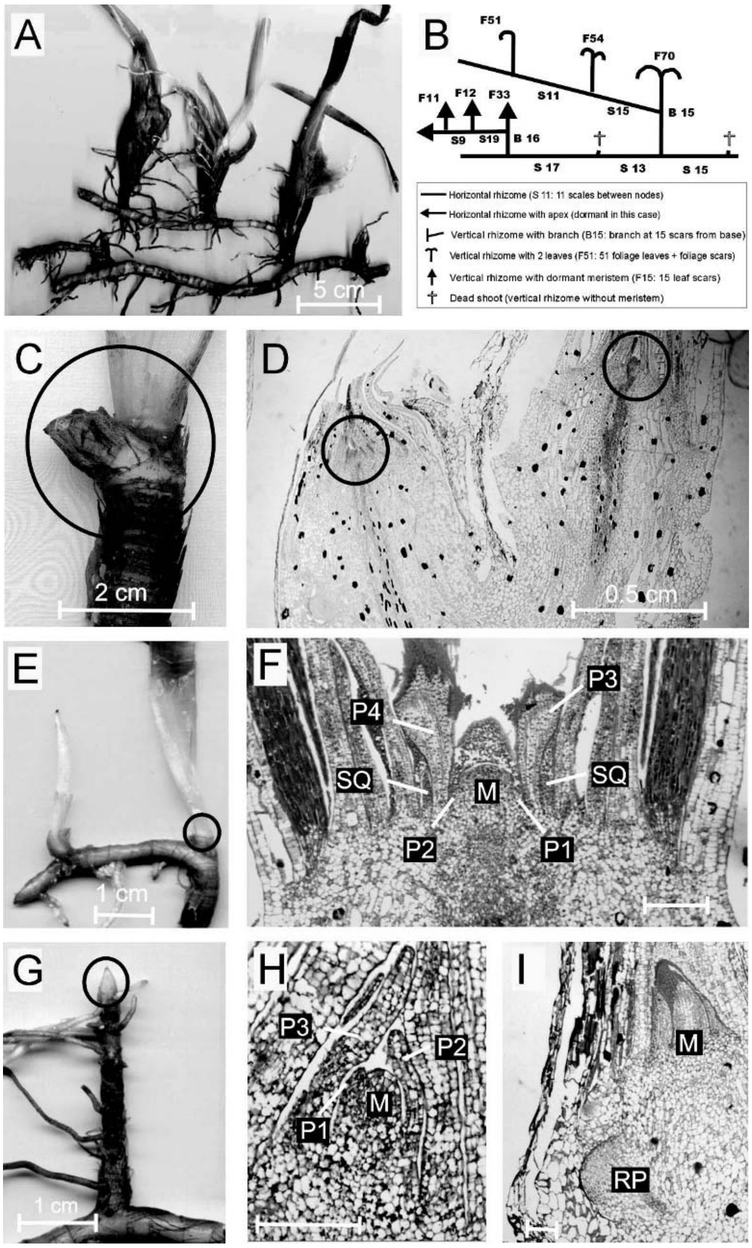

Fig. 1. Thalassia testudinum—specimen from Puerto Morelos reef lagoon, Mexican Caribbean. (A) General habit, showing a horizontal rhizome with a foliage shoot which has formed a lateral branch; on the same rhizome section, a dormant shoot has also branched, (B) Schematic drawing of rhizome section shown in A, (C) Detail of vertical rhizome showing initiation of branching, (D) Transverse section through section (indicated by circle in C), the circles indicate location of the apical meristems (Safranin-fast green tinction, amplification 10 × 1), (E) Lateral branch of a vertical rhizome, showing apex and juvenile shoot, (F). Transverse section through apex of a foliar shoot showing details of the apex (zone indicated by circle in E; Fuelgen tinction, amplification 10 × 4), (G) Dormant shoot; note unilateral position of the roots, (H) Transverse section of the apex of a dormant shoot, note that the scale-like leaves are folded over the meristem (Fuelgen tinction, amplification 10 × 10), (I) Transverse section through dormant shoot in another plane, showing root primordium (Fuelgen tinction, amplification 10 × 10). M: meristem, P: leaf (or scale) primordium, numbers are assigned in order of development, P1 being the youngest. SQ: squamule, RP: Root Primordium. (Nomenclature follows Tomlinson and Vargo, 1966 and van Tussenbroek et al., 2000). Lines in the histological sections represent 0.2 mm. Figs. D, F, H, and I with technical assistance of J.G.R. Wong and C.A. Galindo Rosete.

shoots in patches where *T. testudinum* had suffered die-off in Florida Bay showed 'twinning', which he attributed to abundant light and nutrients conditions. It is possible that under these conditions, apical dominance is low and the branched apex forms foliar tissue, instead of becoming a functional horizontal rhizome apex. On the horizontal rhizomes, branching occurs at regular intervals, and for both *Thalassia* species, the number of scale leaves between each pair of branches is always odd (usually varying between 7 and 19), as the branches are born alternatively left and right (Fig. 1B). The vertical rhizomes, in contrast, branch more sporadically and at irregular intervals (Fig. 1B). Tomlinson (1970) marveled at the highly specialized capacity of the apical meristem of the horizontal rhizome of *Thalassia*, stating that 'it can count, (and) it can distinguish between left and right,' and mentioned that the precise organization of the shoot system sets *Thalassia* apart from the other members of its family and from all other monocotyledonous plants. But this highly organized and rigid growth pattern implies that *Thalassia* depends strictly on the apex of the horizontal rhizome for vegetative expansion, differing in this respect with other seagrass genera, which to a greater or lesser degree have more flexible proliferation patterns, because the distinction between horizontal and vertical axes is less absolute, and, thus, the apical meristems have the potential to produce either horizontal or vertical rhizomes (Tomlinson, 1974).

The strict dependence of the horizontal rhizome apex for clonal expansion, together with the low plasticity in internode length and absence of dormant axillary buds (Tomlinson, 1974), led van Tussenbroek et al. (2000) to raise the question of how *T. testudinum* could respond to changes in resource availability, as this rigid growth pattern apparently does not allow for regulation of the spacing of the resource-acquiring shoots. Although under conditions of high resource availability, this seagrass does show some flexibility in its growth form as was demonstrated by the presence of 'twin shoots', and exceptionally high leaf formation rates in die-off patches in Florida Bay by Durako (1995, see above). Van Tussenbroek et al. (2000) found that the foliar development of the vertical rhizomes of *T. testudinum* in a reef lagoon with a limited nutrient supply, was inhibited at increasing rhizome density, but that the meristems of these vertical rhizomes maintained functionality by forming scale-like foliar structures instead of foliage leaves. Van Tussenbroek et al. (2000) named these structures 'dormant meristems' (Figs. 1G–I). The existence of such a 'dormant-meristem bank' allowed the seagrass to exploit a sudden increase in resources (provided as nutrient application to the sediments) through reactivation of the foliar development of these dormant meristems, before other plant species could invade the area. Apparently, the dormant apical meristems have the same function as the dormant axillary buds in most other clonal species, with the advantage that an apical meristem can pass through the stages of dormancy and foliar reactivation at various times during its life. It is important to note, however, that dormant meristems have also been registered under adverse climatic conditions; for example Pérez and Galindo (2000) reported a mass defoliation of *T. testudinum* in Venezuela (total area 320 km^2) after a short episode of extreme low salinity caused by torrential rain. The underground rhizomes were left intact, and had many dead but also defoliated dormant shoots. Reactivation of the foliar development of these dormant shoots allowed for a complete recovery of these meadows within 5 months.

Extension of the horizontal rhizome of *Thalassia* spp. is slow in comparison with that of many other seagrass species (Marbà and Duarte, 1998); rates of horizontal rhizome extension in *T. testudinum* vary between 19 and 35 cm $year^{-1}$ $apex^{-1}$ depending on the sampling site (Gallegos et al., 1993; van Tussenbroek, 1998), and those of *T. hemprichii* vary between 21 and 56 cm $year^{-1}$ $apex^{-1}$ (Vermaat et al., 1995; Rollon et al., 2001). The restricted growth pattern of *Thalassia* spp. (see above), combined with these slow expansion rates, poses restrictions for recolonization of cleared areas due to disturbances. Dawes et al. (1997) found that the regrowth of *T. testudinum* in clearances caused by propellors in Tampa Bay was slow due to limited production of horizontal rhizome meristems, and could not be attributed to changes in sediment conditions due to the clearing of the seagrasses. These authors estimated a recovery period of 2.3–4.1 year, which is in accordance with the observation of Zieman (1976), that tracks by propellors persisted for 2–5 year in *T. testudinum* beds in Biscayne Bay, Florida. Durako et al. (1992) estimated that *T. testudinum* required between 3.6 and 6.0 year to obtain pre-disturbance densities experimental propellor scars in Tampa Bay, and Williams (1990) found that *T. testudinum* required more than 4.3 year to obtain pre-cleared density in 1 m^2 denuded experimental plots in the US Virgin Islands.

Similar rates are reported for *T. hemprichii* in the Philippines by Rollon et al. (2001), who found that this species required ~2 year to achieve previous values of abundance in 0.25 m^2 plots after experimental clearance in a mixed species seagrass meadow.

Clonal growth implies that the ramets (sensu Harper, 1977, which can considered to be the shoots for seagrasses) have the potential to live independently (van Groenendael and de Kroon, 1990). A clone is defined here as a group of ramets which are physically interconnected, which may or may not be integrated physiologically. For *Thalassia*, various studies suggest that neighboring shoots of a clone show physiological integration. Tomasko et al. (1991) transplanted sections of rhizomes with different numbers of shoots, and found that a minimum number of two shoots per section was required for survival, but that sections of four shoots showed significantly more proliferation (that is formation of new horizontal rhizome apices through lateral branching of the vertical rhizomes of the shoots). Dawes et al. (1997) found that shoots at the edges of damaged rhizomes showed equal leaf growth as shoots within the adjacent meadow, indicating that they were supported by other interconnected shoots within the meadow. These latter two studies suggest that resource sharing by interconnected ramets plays a large role in the functioning of *T. testudinum*, which is supported by experimental data. Tomasko and Dawes (1989) experimentally shaded shoots, which were either allowed to remain connected via the rhizome (control treatment) or disconnected by cutting the horizontal rhizome. Isolated shaded shoots had lower blade growth rates as well as lower protein and soluble carbohydrate contents than shoots of the control treatment. In a subsequent study, Tomasko and Dawes (1990) tested whether the degree of shoot interdependence varied with season along a depth gradient, and found that there was an effect of shoot isolation on blade growth (blade growth rates of experimentally isolated shoots were significantly lower than those of interconnected ones), in the summer but not in autumn. They also found that shoot integration diminished with depth, which they attributed to a combination of the more homogeneous light environment at greater depths (all shoots are exposed to similar conditions), or depth-related differences in shoot dynamics (all shoots are stressed due to limitations of the primary resource). These authors reported that translocation occurred mainly in direction to the active rhizome apices, which was confirmed by Marbà et al. (2002), who followed incorporation of ^{13}C and ^{15}N in the clones of various seagrass species. They found that the resources from a labeled shoot of *T. hemprichii* provided the heavy C and N isotopes to 7 shoots which corresponded to a translocation distance of ~28 cm in acropetal direction, and to 4 shoots (~12 cm) away from the apex. The shoots were able to share with their neighbors ~27 and 17% of the incorporated ^{13}C and ^{15}N, respectively, within 4 day. These few studies of physiological integration in *Thalassia* spp. have focused on the redistribution of resources from shoots located in sites of resource abundance to shoots located where resources are scarce (Hartnett and Bazzaz, 1983; Alpert and Mooney, 1986). However, physiological integration reaches further than mutual support of stressed ramets (sensu Harper, 1977) by unstressed ones, and it would be interesting to direct future research efforts into questions of clonal foraging, i.e. selective placement of resource-acquiring structures in favorable habitat patches (Hutchings and de Kroon, 1994), or possible benefits of clonal growth in heterogeneous vs. homogeneous environments (Hutchings and Wijesinghe, 1997).

B. Sexual Reproduction

The flowers of *Thalassia* are produced in the axils of the foliage leaves. As with many other seagrasses, both species of this genus are dioecious; the male and female flowers being produced by different clones (Cox and Tomlinson, 1988). The female flowers of *T. testudinum* have 7–8 styles, whereas those of *T. hemprichii* have 6: the stigmatic branches are considerably longer in *T. testudinum* than in *T. hemprichii*. The number of stamens of the male flowers is 9 in *T. testudinum* and between 3 and 12 (mostly between 6 and 9) in *T. hemprichii*. Male flowers usually occur in groups of two or three (but up to five flowers per florescence have been recorded), whereas the female flowers usually occur singly, and occasionally as a pair (Durako and Moffler, 1985a). The flowers barely rise above the substratum, and according to Cox and Tomlinson (1988), male floral anthesis and dehiscence of anthers is nocturnal, releasing round pollen grains embedded in ~1.2 mm long mucilage strands, whereas anthesis in female flowers is not necessarily restricted to nocturnal hours. Flowers are not uncommon for either species of *Thalassia* (Table 2). In most locations, flowering is clearly seasonal (Table 3), but Durako and Moffler (1987a) on one occasion,

Table 2. Flowering frequency of *Thalassia* spp. in different geographical areas. The sites are ordered according to a N–S gradient.

Reference	Place	Density of inflorescences	Male: Female shoots
T. testudinum			
McMillan (1976)	Redfish Bay, Texas (27°48′N)	None	–
Durako and Moffler (1985a) (spatial variation)	Tampa Bay (27°45′N)	nd	1.40:1–1.71:1
Kaldy and Dunton (2000) (inter-annual variation)	Laguna Madre, Texas (28°08′N)	13–30%	nd
Grey and Moffler (1978) (spatial variation)	Tampa Bay, Florida (27°45′N)	8–19 shoots m^{-2} (2.3–6.8%)	0.33:1
Durako and Moffler (1987a) (annual variation)	Tampa Bay, Florida (27°36′N)	53–152 shoots m^{-2} (10.0–29.4%)	0.35:1–1.87:1
Witz and Dawes (1995) (spatial variation)	Tampa Bay (27°45′N)	3–21%	0.5:1–2.14:1
Orpurt and Boral (1964)	Biscayne Bay, Florida (25°33′N)	∼1%	Approximately 1:1
Tomlinson (1969b)	Biscayne Bay, Florida (25°33′N)	nd	4:1
Peterson and Fourqurean (2001) (spatial variation)	Florida Keys (24°45′N)	0–25%	nd
Durako and Moffler (1985a) (spatial variation)	Florida Keys (24°36′N, 24°42′N)	nd	0.32:1–2.00:1
Gallegos et al. (1992)	Caribean, Mexico (21°08′N)	6.2 shoots m^{-2}	nd
van Tussenbroek (unpublished) (spatial variation)	Caribbean, Mexico (21°08′N)	2.5–47.5%	0.3:1–8.0:1
Cox and Tomlinson (1988)	St. Croix (17°45′N)	55.7 flowers m^{-2}	Approximately 20:1
T. hemprichii			
Duarte et al. (1997b) (interannual mean)	Philippines (16°27′N)	12.5%	nd
Rollon et al. (2001) (spatial variation)	Philippines (11°03′N)	27–29%	nd

Table 3. Reproductive season of *Thalassia* spp. in different geographical areas (ordered from N to S).

Reference	Place	Flowering season	Time of peak reproduction
T. testudinum			
Kaldy and Dunton (2000)	Laguna Madre (28°08′N)	April–August (flowers/fruits)	April–May (flowers)
Durako and Moffler (1987a)	Tampa Bay (27°45′N)	spring-July (flowers/fruits)	June (flowers)
Orpurt and Boral (1964)	Biscayne Bay (25°33′N)	April–September (flowers/fruits)	nd
van Tussenbroek (unpublished data)	Mexico (21°08′N)	March–August (flowers / fruits)	April (flowers) July (fruits)
García et al. (1998)	Puerto Rico (18°01′N)	March–June (flowers?)	April–May (flowers)
Cox and Tomlinson (1988)	US Virgin Isl. (17°45′N)	March–May (flowers)	nd
Varela et al. (1998)	Venezuela (10°52′N)	nd	May (flowers) July (fruits)
T. hemprichii			
Duarte et al. (1997b)	Philippines (16°27′N)	October–January (flowers)	November (flowers)
Rollon et al. (2001)	Philippines (11°03′N)	November–May (flowers / fruits)	January (flowers)
Parthasarathy et al. (1991)	Southern India (8° 25′–8° 06′N)	April (fruits)	nd
Verheij and Erftemeijer (1993)	Indonesia (5 0–5 10 S)	All year (excl. January and June–July)	nd
Brouns (1985)	Papua New Guinea (9°30′S)	June–January (flowers) All year, excl. March–April (fruits)	August (fruits)

reported early stage inflorescences in October in Tampa Bay, and Moffler et al. (1981) observed early-stage fruits in midwinter, which is outside the normal flowering season for this region. Male and female clones usually grow intermixed, but Durako and Moffler (1985a) reported spatial segregation of *T. testudinum* sexes at one site in Tampa Bay, with female clones growing in shallower waters than males. They suggested that this segregation may reflect the age structure of the seagrass meadow, with the male shoots being older than females, but it is also possible that females occur in shallower waters because they have higher light demands, and more studies are necessary. In another study, Durako and Moffler (1985b) reported that in Tampa Bay, shoots with male flowers had broader leaves than those having female inflorescences, suggesting that sexual dimorphism may occur in this species, but in this case also, further studies are required to establish this. The diameter of mature fruits is between 20 and 25 mm (Kuo et al., 1991; van Tussenbroek, unpublished data). The number of seeds per fruit is usually two or three in both species, but can vary from one to six (Orpurt and Boral, 1964; Kuo et al., 1991; Kaldy and Dunton, 2000; Rollon et al., 2001).

The seeds are rich in proteins and starch; germination is precocious and they form a shoot apex with leaf primordia (or intraseminal leaves) while still within the fruit (Orpurt and Boral, 1964; Moffler and Durako, 1984; Kuo et al., 1991). Thus, the seeds are cryptoviviparous (zygotes develop significantly but do nor penetrate the fruit pericarp before dispersal: *sensu* Tomlinson, 1986), with no dormancy period. Seeds are negatively buoyant, but may float for a short period immediately after fruit dehiscence, as was reported for *T. testudinum* by Kaldy and Dunton (1999; buoyant <1 day) and for *T. hemprichii* by Lacap et al. (2002; median time of buoyancy 0.3 h). The seeds are released from the disintegrating fruits (which are positively buoyant) either before or after these becomes detached from their peduncles (Orpurt and Boral, 1964; Kuo et al., 1991). Thus they can be deposited within or outside the mother meadow, which increases the potential for seed dispersal. Lacap et al. (2002) found that seeds moved $\sim$100 cm day^{-1} over the sediment within a *T. hemprichii* bed in a Philippine reef flat system. These seeds disappeared from their experimental area within 2–3 day, which they thought to be due to herbivory or burial by invertebrates. Floating fruits, on the other hand, have a considerably higher dispersal capacity and Kaldy and Dunton (1999) estimated a dispersal distance of $<$1.5–15 km for detached fruits of *T. testudinum* in the Laguna Madre, Texas. And Lacap et al. (2002) recorded a mean in situ dispersal speed of 0.43 km h^{-1} for floating fruits of *T. hemprichii*, which combined with a flotation time between 2 and 7 day, corresponded with a dispersal distance of 23–74 km.

It is not uncommon to report young seedlings ($<$1-year old) unattached or anchored in the field (Lewis and Phillips, 1980; Williams and Adey, 1983; Kaldy and Dunton, 1999), but very few survive in the long term (Kaldy and Dunton, 1999), although seedlings seem to be able to survive quite well under laboratory conditions (Williams and Adey, 1983; Moffler and Durako, 1984; Durako and Moffler, 1981, 1984, 1987b; Kaldy and Dunton, 1999). Field studies have reported that population expansion and maintenance of *Thalassia* spp. occurs almost exclusively through vegetative propagation (see above), and rarely through successful establishment of seedlings. Although recently, Kaldy and Dunton (1999) found that seedling establishment was important for the expansion of *T. testudinum* meadows in Laguna Madre, Texas, and Whitfield et al. (2004) reported that seedlings of *T. testudinum* were common source of new recruits in physically disturbed areas (by a grounded vessel and scarring of beds by propellers of small boats) of seagrass beds in the Florida Keys.

Currently, the principal role of sexual reproduction in the evolution of these two species is not clear. Sexual reproduction might play a role in maintenance of genetic variability within populations, or on the other hand, its major role may be the recolonization of areas from which the seagrass has been eradicated by major disturbances (rescue effect, Ouborg et al., 1999), but data to support either hypothesis are still insufficient. In this context it is important to note that long-distance dispersal by vegetative fragments has been reported for some seagrass species (Cambridge et al., 1983; Kuo et al., 1987; Campbell, 2003), but colonization of virgin areas by fragments has never been reported for either *Thalassia* species. An exceptional study is that of Rollon et al. (2001) who discovered a disjunctive and young population (average shoot age $\sim$1 year) of *T. hemprichii* on an island of the Kalayaan Island group in the Indo-Pacific ocean, $>$500 km away from major populations of this species. Interestingly, seven other nearby islands within 10s of km distance, did not show signs of seagrass colonization.

Possible explanations for the existence of this disjunctive population were that floating fruits from existing populations reached the island (improbable, as this would take ~2 months), or 'hitch-hiking' of fruits or seeds in ballast water of ships or transported coastal sediments (Rollon et al., 2001).

VII. Population Dynamics

A. Demography

To date, demographic analyses of the genets (an individual originated from a seed, sensu Harper, 1977) of *Thalassia* have not been attempted because following a genet in the field is virtually impossible. Tracing the shoots of an individual in the field is difficult because their interconnecting horizontal rhizomes occur belowground and are entangled. Also, the connections between the shoots break with time, either through mechanical damage or decay of the oldest end of the horizontal rhizomes, thus a genet consists of many separate rhizomes sections (i.e. clones), and it is impossible to tell one genet apart from another. In contrast, the shoots arising from the horizontal rhizomes, which can considered being the ramets (sensu Harper, 1977), are easily identified, and techniques of age determination of the shoots (Patriquin, 1973; Duarte et al., 1994) make it possible to study their demography.

The longevity of the shoots can be determined by 'translating' their size (expressed as the number of scars of abscised leaves) into age using information based on the number of leaves produced yearly. For example, a shoot with 30 leaf scars plus standing leaves, which produces ten leaves per year, has an age of 3 years. There exist various techniques for the determination of annual leaf production, or its derivative, annual mean Plastochron Interval, which was defined by Patriquin (1973) as the difference in age between two successive leaves, measured when they have reached the same stage of development. The techniques applied to *Thalassia* spp. are: (1) Leaf marking, which determines the rate of leaf initiation per foliar shoot (Durako, 1994; van Tussenbroek, 1994a; Kaldy et al., 1999; Peterson and Fourqurean, 2001), (2) differences in internode's length of the vertical rhizomes (Gallegos et al., 1993; Marbà et al., 1994), (3) number of leaves formed between successive flower scars (Gallegos et al., 1992; van Tussenbroek, 1994a), and (4) annual cohort analysis based on size frequency histograms of the vertical rhizomes (Durako, 1994; Duarte et al., 1994). All of these techniques, except for leaf marking, utilize cyclical variations caused by seasonal differences in vertical rhizome morphology to indicate the passage of a year, and the number of leaf scars between these seasonal imprints is considered to be the number of leaves produced in that year. The important underlying assumption of all techniques of age-determination is that the number of leaves produced annually does not differ significantly between years, but only a few authors have tested this, and results vary from place to place. *T. testudinum* showed large inter-annual variability in annual leaf formation rates in the Laguna Madre, Texas (Kaldy et al., 1999), whereas this species showed similar annual rates of leaf production over a period of 13 years in a tropical Mexican reef lagoon (van Tussenbroek, 2002), and neither Durako (1994) nor Peterson and Fourqurean (2001) found significant differences in annual mean leaf emergence rates between two consecutive sampling years at a large number of sites in Florida Bay.

The ideal study of shoot demography would be to mark a large number of shoots and follow their development through time, allowing for production of a dynamic life-table, but this requires excavation of the rhizomes, which is virtually impossible without considerable damage. Therefore, all demographic studies have involved examination of the shoot population sampled at one particular time, resulting in a static age-distribution. Applications of such static age-distributions have been many-fold; and amongst others they have been used to retrospectively assess flowering events and the effects of a hurricane on *T. testudinum* in the Mexican Caribbean (Gallegos et al., 1992; Marbà et al., 1994; van Tussenbroek, 1994a,b). The principal application of the static age-distributions has been for the derivation of population growth rate and related parameters (such as mortality, recruitment, shoot turnover rates, and half life), according to the model proposed by Duarte et al. (1994), which has been used for populations of both *T. testudinum* (Gallegos et al., 1993; Durako, 1994; Peterson and Fourqurean, 2001) and *T. hemprichii* (Vermaat et al., 1995; Rollon et al., 2001). There are questions, however, over whether these static models can be applied to determine population growth (see Durako and Duarte, 1997; Jensen et al., 1997; Kaldy et al., 1999; van Tussenbroek, 2000), or whether the prerequisites of constant annual shoot mortality and recruitment rates and age-independent mortality, required by this model are tenable (Jensen et al., 1996; Kaldy et al., 1999; van Tussenbroek, 2000; Peterson and Fourqurean, 2001). Another application of shoot demography has been that of van Tussenbroek (2002), who applied a classic static life-table analysis to various stable shoot-populations of *T. testudinum*, and found that mortality of the shoots was age-dependent, with lower mortality for the younger shoots. This is not uncommon for clonal plants, and is an indication of support of the younger ramets by the older ones (Sarukhán and Harper, 1973; Hartnett and Bazzaz, 1983). Also, elasticity analysis of a derived Leslie matrix showed that ramification of 1-year-old shoots was by far more important to net population growth than survival of the foliar shoots of all other age classes. The latter indicates that proliferation through branching is not only important for expansion of populations to nearby virgin areas (see above), but also for maintenance of established *Thalassia* populations.

B. Population Genetics

The first study on population genetics on both species of *Thalassia*, was that by McMillan (1980), who found that allozymes separated the two species *T. testudinum* and *T. hemprichii*, but did not detect any intra-specific variability for either species throughout their distribution area. Since this pioneering work, attempts have been made to separate populations of *T. testudinum* using allozyme, RAPD, ISSR-DNA Fingerprinting, or AFLP techniques. Schlueter and Guttman (1998) employed fourteen allozymes of which five proved to be polymorphic, and found that the population in the Florida Keys consisted of at least four genets. However, across all sampling sites, they reported low genetic diversity (>0.975 similarity) and high gene flow over large distances (>120 km). This tendency was confirmed by Kirsten et al. (1998), who employed RAPDs for comparison of populations from N-Florida, the Florida Keys, and Jamaica. These authors found high genetic variability on a local scale (81%), whereas only 19% of the variation was explained by divergence on a macro-geographical scale. Davis et al. (1999) used the more unusual technique ISSR (Inter Sample Sequence Repeat) DNA Fingerprinting to determine the genetic variability of *T. testudinum* in an area of $\sim$25 km^2 in Florida Bay; they reported 22 genetically distinct individuals out of the 72 sampled shoots, and different individuals were found on small spatial scales (half of the genetic variability was within $\sim$25 cm distance), suggesting that the clones grow intertwined. More recently, Waycott and Barnes (2001) applied the AFLP (Amplified Fragment Length Polymorphism) technique to differentiate populations from San Blas, Panama, and Bermuda. AFLP is a relatively new fingerprinting technique, and has a higher resolution than RAPDs. Even with this technique they found a very low degree of differentiation of genotypes between Panama and Bermuda in spite of the fact that the sites are separated by 2700 km, and only 5.4% of the genetic variability was attributed to the sites between the regions. In summary, all studied populations of *T. testudinum* were multiclonal, but inter-population genetic diversity was low, suggesting a high gene flow between populations. Suggested reasons for the high genetic uniformity of populations which are up to hundreds or thousands km apart, have been long-distance movement of vegetative, or transport of sexual offspring over large distances on a geographical scale (Kirsten et al., 1998; Waycott and Barnes, 2001; Waycott et al., Chapter 2).

VIII. Community Ecology

A. Vegetation Structure

The structure of seagrass communities in general is regarded as quite simple, as it consists of one or a few seagrass species of a rather similar morphology (den Hartog and Phillips, 2001). *Thalassia*-dominated seagrass meadows, however, are generally multi-taxon conglomerates composed of various species of seagrasses, rooted calcareous and fleshy algae (rhizophytic algae), drifting fleshy or filamentous algae, and epiphytes (Tables 4 and 5). The rhizophytic calcareous algae often form an important component of these communities, which together with the calcareous epiphytes (see section 2), are important producers of carbonate sediments in many tropical localities (Land, 1970; Bosence, 1989). For example, psammophytic species *Halimeda incrassata* produces generally in the order of tens or hundreds gram calcium carbonate per year depending on the locality (Bach, 1979; Wefer, 1980; Multer, 1988; Payri, 1988; Freile and Hillis, 1997). These carbonate sediments are subsequently trapped and bound by the seagrasses (Scoffin, 1970). In the Western

Table 4. Prominent macrophytes associated with _Thalassia testudinum_ in the Western Atlantic, excluding those on hard substratum within these meadows. Not all species occur throughout the distribution range of _T. testudinum_, and they are never all encountered in a single meadow. The species diversity of the meadows may vary considerably from site to site. From Dawes et al. (1995), Kuenen and Debrot (1995), UNESCO (1998), and Littler and Littler (2000). Seagrasses according to Green and Short (2003). *Rooted vegetation frequently reported in association with _T. testudinum_.

T. testudinum	
Other seagrasses	_Halodule wrightii*, Halophila bailoniii, H. decipiens, H. engelmannii, H. johnsonii_ (conspecific _with H. ovalis), Syringodium filiforme*_
Rooted (rhizophytic) macroalgae	**Calcareous (Chlorophyta):** _Halimeda discoidea, H. incrassata,*, H. lacrimosa, H. monile*, H. opuntia*, H. scabra, H. simulans*, Penicillus capitatus*, P. dumentosos*, P. lamourouxii, P. pyriformis, Rhipocephalus oblongus*, R. phoenix*, Udotea abbottiorum, U. cyathiformis, U. fibrosa, U. flabellum*, U. luna, U. spinulosa, U. wilsonii_ **Non-calcareous (Chlorophyta):** _Caulerpa ashmeadii, C. cupressoides, C. lanuginosa, C. mexicana, C. paspaloides, C. prolifera, C. sertularioides, C. verticillata, Avrainvillea digitata, A. longicaulis, A. mazei, A. nigircans, A. rawsonii, A. silvana, Cladocephalus luteofuscus, Rhipilia tomentosa_
Drift algae., incl. common lithophytic or epiphytic algae frequently torn loose from substratum (taxa until genus level)	**Chlorophyta:** _Acetabularia, Anadyomene, Batophora, Bryopsis, Bryothamnion, Chaetomorpha, Cladopheropsis, Cladophora, Dictyosphaeria, Enteromorpha, Mycrodictyon, Neomeris, Valonia_ **Rhodophyta:** _Acantophora, Amphiroa, Centroceras, Ceramium, Champia, Chondria, Euchema, Galaxaura, Gracilaria, Halydictyon, Hypnea, Jania, Laurencia, Liagora, Neogoniolithon, Spyridia_ **Phaeophyta:** _Dictyota, Lobophora, Padina, Sargassum, Sporochnus, Turbinaria,_ **Cyanophyta:** (various filamentous taxa)
Epiphytes	See: Sullivan (1979: diatoms), Humm (1964: 113 species) and Ballantine and Humm (1975: 66 species on 4 seagrass species)

Atlantic, _Thalassia testudinum_ is the only seagrass species present in some areas, but it more often coexists with _Syringodium filiforme_, _Halodule wright,_ and occasionally it is found accompanied by other seagrass species (Table 4). In the Indo-Pacific, the seagrass meadows are usually more complex, as species richness of the seagrasses is much higher in this region than in the (sub-)tropical Atlantic (Table 5). _T. hemprichii_ can be the only seagrass species present, it can dominate in mixed seagrass meadows (Ogden and Ogden, 1982; Brouns and Heijs, 1985; Heijs, 1987; Poiner et al., 1989; Tomasko et al., 1993; Vermaat et al., 1995; Duarte et al., 1997a; Jagtap, 1998; Rollon et al., 1998) and it can form an insignificant component of meadows dominated by other seagrasses (Birch and Birch, 1984; Brouns and Heijs, 1985). Usually, _Thalassia_-dominated meadows are continuous and cover considerable areas, but in some areas these meadows are alternated with monospecific patches of other seagrasses such as _Halodule wrightii_ (Garzón-Ferreira, 1998; Rose and Dawes, 1999), _Syringodium filiforme_ (Garzón-Ferreira, 1998), or _Halophila_ spp. (Garzòn-Ferreira, 1998; Nakaoka and Izumi, 2000).

Zonation in coastal areas, where _Thalassia_ dominates, follows the ‘classical’ pattern of small and narrow leaved species in the intertidal, which in the shallow subtidal become replaced by the more broad-leaved _Thalassia_ (den Hartog and Phillips, 2001). In deeper waters, _Thalassia_ is replaced again, either by smaller seagrass species or macroalgae (often psammophytic _Halimeda_ spp.). In the Western Atlantic, at places with a clear downward gradient of the sea bottom and available substrate, a small band consisting of _Halodule wrightii_ or _Halophila decipiens_ toward the landward side usually precedes _Thalassia testudinum_-dominated communities. In areas with consistent disturbance and unstable sediments, which are low in organic content, _S. filiforme_ may be the most abundant seagrass, where it is commonly found in a fringe at beaches. Deeper down the slopes of the Atlantic coasts, _T. testudinum_ is replaced by _S. filiforme_ or _H. wrightii_ that tolerate lower light levels (Buesa, 1975; Zieman, 1982; Kuenen and Debrot, 1995). In the Indo-Pacific, various _Halophila_ spp, _Halodule pinifolia_ and _Cymodocea_ spp may occur before _T. hemprichii_ toward the coastline. Seagrass species such as _Halodule uninervis, Cymodocea_

Table 5. Prominent macrophytes associated with *Thalassia hemprichii* in the Indo-Pacific, excluding those on hard substratum within these meadows. Not all species occur throughout the distribution range of *T. hemprichii*, and they are never all encountered in a single meadow. The species diversity of the meadows may vary considerably from site to site. From: Poiner et al. (1989); Brouns and Heijs (1985); Heijs (1985a, 1987); Jagtap (1991, 1996); Ogden and Ogden (1982); and Rodrigues et al. (1997). Seagrasses according to Green and Short (2003). *Rooted vegetation frequently reported in association with *T. hemprichii*.

T. hemprichii	
Other seagrasses	*Cymodocea serrulata*, C. rotundata*, C. angustata, Halodule uninervis*, H. pinifolia, Enhalus acoroides*, Halophila beccari, H. decipiens, H. minor, H. ovalis*, H. ovata, H. spinulosa, H. stipulacea, H. tricostata, Syringodium isoetifolium*, Thalassodendron ciliatum*
Rooted (rhizophytic) macroalgae	**Calcareous (Chlorophyta):** *Halimeda cylindracea, H. discoidea, H. gracilis, H. incrassata*, H. macroloba, H. opuntia*, H. simulans, H. taenicola, H. tuna, Udotea orientalis* **Non-calcareous (Chlorophyta):** *Avrainvillea erecta*, A. lacerate, Caulerpa cupressoides, C. serrulata, C. sertularioides*, *C. taxifolia*
Drift algae, incl. common lithophytic or epiphytic algae frequently torn loose from substratum (taxa until genus level)	**Chlorophyta:** *Acetabularia, Anadyomene, Boergesenia*, *Boodlea, Bornetella, Chaetomrpha, Chlorodesmis, Cladophora, Codium, Dictyosphaeria, Enteromorpha, Mycrodictyon, Neomeris, Struvea, Ulva, Valonia, Valoniopsis* **Rhodophyta:** *Acanthophora, Acrochatium, Actinitrichia, Amansia, Amphiroa, Asparagopsis, Centroceras, Ceramium, Ceratodicton, Champia, Euchema, Galaxaura, Gelidium, Gelidiopsis, Gelidiella, Gracilaria, Hypnea, Jania, Laurencia, Leveillea, Liagora, Polysiphonia, Porteira, Soliera, Spyridia, Tolypiocladia* **Phaeophyta:** *Chnoospora, Colpomenia, Cystophyllum, Dictyota, Dictyopteris, Hincksia, Hydroclathrus, Lobophora, Padina, Rosenvingea, Turbinaria, Sargassum* **Cyanophyta:** (various filamentous taxa)
Epiphytes	See: Heijs (1983, in Heijs, 1985b: 83 species), Jagtap (1998: 15 common species), Uku and Björk (2001: 10 common species); Sterrenburg et al. (1995: diatoms)

serrulata, and at places *Enhalus acroides,* grow below the lower depth range of *T. hemprichii* (Ogden and Ogden, 1982; Brouns and Heijs, 1985). Past the point at which the larger species can occur (generally > 8–10 m), fine carpets of *Halophila spp.* (principally *H. decipiens*, *H. engelmanii* in the W-Atlantic, and *H. decipiens*, *H. ovalis* and *H. spinulosa* in the Indo-Pacific) can be found extending to past 30–40 m in depth.

B. Interactions between Plants

1. Rooted Plants (Seagrasses and Rhizophytic Algae)

Considering that most seagrass beds dominated by *Thalassia* spp. are multi-taxon conglomerates, it is amazing that very few studies have dealt with interactions between the plants that compose the seagrass beds. In particular, interactions between the rooted species have received little attention. Amongst the few experimental studies to examine inter-specific interference between seagrass species is that of Williams (1987), who tested the effect of *T. testudinum* on *S. filiforme* in the U.S. Virgin Islands.She found that *T. testudinum* had a negative effect on the production of *S. filiforme* and that belowground competition for nutrients was more important than shading by the leaf canopy of *T. testudinum*. A surprising result was a positive interaction between these two species, in that the leaf canopy of *T. testudinum* protected *S. filiforme* leaves from breaking. In Tampa Bay, Rose and Dawes (1999) found that *T. testudinum* growing in patches intermixed with *H. wrightii* had reduced growth and biomass in comparison with monospecific patches. Fourqurean et al. (1995) reported that *H. wrightii* competed successfully with *T. testudinum* under high-nutrient conditions, and replaced the latter seagrass after 8 years of fertilization of a seagrass meadow in Florida Bay. Under lower-nutrient conditions, *H. wrightii* often occurs during the early stages of succession to be replaced in time by *T. testudinum,* which is considered to be the climax species and competitively superior (see section 6.3). Fourqurean et al. (1995) explained the dominance of *H. wrightii* in their study by the higher nutrient demand of *H. wrightii* than that of *T. testudinum*; and during succession *T. testudinum* replaces *H. wrightii* due to its capacity to draw nutrients down to concentrations below the requirements of the latter seagrass. Davis and Fourqurean (2001) demonstrated that there is competition for nutrients between co-occurring *T. testudinum* and the rhizophytic calcareous alga *Halimeda incrassata* in the Florida Keys. The presence of seagrass decreased the size of the algal thalli by 20% but the algae only decreased *T. testudinum* shoot size by 10%. Tissue nitrogen of *T. testudinum* decreased in the presence of *H. incrassata*, suggesting that nitrogen competition was the mechanism of interaction. In Thailand, Nakaoka and Izumi (2000), studied interference at patch level for the seagrasses *T. hemprichii* and *Halophila ovalis*. They found that *H. ovalis* had higher biomass and lower production in the center than at the edges of the patches joining unvegetated areas, whereas these differences between center and edge were not detected when the *H. ovalis* patches joined *T. hemprichii*.

Rose and Dawes (1999) studied intra-specific interference in shoots of *T. testudinum* by comparing their leaf mass and growth in low and high-density monospecific meadows. They reported that in high-density monospecific meadows growth and biomass of the shoots were reduced (compared with lower density meadows), suggesting that the foliar shoots competed for available resources. Van Tussenbroek et al. (2000) reported inhibition of foliar development at high-rhizome density in *T. testudinum*, and found that the spacing of foliar shoots was regulated just below the critical density at which negative effects on foliar development would occur, which is quite common for clonal plants (Hutchings, 1979). The shoots in which development was inhibited became dormant. Subsequent foliar development of these dormant shoots after experimental fertilization suggests that competition for belowground nutrients played a significant role in the inhibition of the development of foliage leaves. These findings are in apparent contrast with the findings of Rose and Dawes (1999), who found that reduction of light by dense leaf canopies was a likely mechanism of intraspecific competition at high densities. However, it has to be borne in mind that these studies were carried out in contrasting areas, the first an oligotrophic reef lagoon, and the second a mangrove-lined estuary.

2. Drifting and Epiphytic Algae

Drifting (free-living, detached, unattached or loose-lying) algae can form extensive mats on top of, or occasionally in between the seagrasses. These mats may remain stationary on the seagrass meadows for days, weeks, or even months, and Bell and Hall (1995) found a clear relationship between the occurrence of drifting masses in *T. testudinum* meadows and sediment grain size, which in its turn is determined by hydrodynamic regimes. Alternatively, the drift algae in or close to *T. testudinum* vegetation may form balls in response to the constant rolling caused by water movement (Littler and Littler, 2000). These balls are assemblages with one to four dominant species and are hollow, the cavity housing a wide variety of invertebrates (Ballantine et al., 1994). Epiphytes may contribute up to 24% of the total aboveground biomass of *Thalassia* meadows (Heijs, 1984), and include a diatom and a macro-algal component. Both drifting algal mats and epiphytes inhibit growth of *Thalassia* (Tomasko and Lapointe, 1991; Holmqvist, 1997), and possible mechanisms of these interactions are shading and smothering of the host plant, and competition for nutrients and gases (van Montfrans et al., 1984; Lapointe et al., 1994; Duarte, 1995). There are indications that the associated fauna of the seagrass meadows increases in number and diversity at higher degree of structural complexity of the seagrass meadows through the presence of epiphytes and drifting algal masses (Gore et al., 1981; Stoner and Lewis, 1985), but long-term cover with high density mats of drifting algae in a *T. testudinum* community resulted in a decrease in associated fauna (Holmqvist, 1997). The abundance of epiphytes and drift algae is often mediated by nutrients and grazers (Lapointe et al., 1994; Heck et al., 2000; Peterson and Heck, 2001), which is also dealt with elsewhere in this chapter (sections 6.4 and 7).

C. Vegetation Succession

The sequence of succession in the seagrass beds generally involves early species that stabilize the sediments and increase the sediment nutrient content, and by doing so allow establishment of later species (Clarke and Kirkman, 1989; Williams, 1990). This

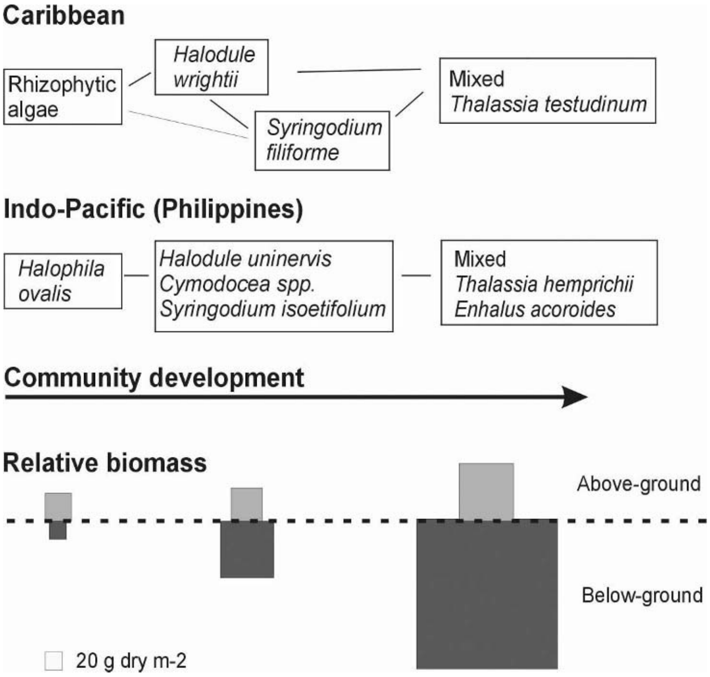

Fig. 2. Idealized schemes of succession leading to a Thalassia dominated community, in the Caribbean (modified from Zieman, 1982), and the Indo-Pacific (after a Philippine community described by Rollon et al., 1998). Later stages in succession usually contain specimen of the earlier stages. The relative biomass diagram only approximates above- and belowground biomass proportions, modified after Zieman (1982) with information from UNESCO (1998) and Duarte and Chiscano (1999) for the Caribbean and Indo-Pacific species, respectively.

suggests that succession in these beds follows the facilitation model, as is the case for many terrestrial plant communities, but uncommon for hard-bottom coastal marine areas (Connell and Slayter, 1977).

In the tropical Western Atlantic, the sequence of succession is initiated, within a few months, by rhizophytic macroalgae (Fig. 2, Patriquin, 1975; Zieman, 1982; Williams, 1990), most commonly species of *Halimeda* and *Penicillus*, although other species of rhizophytic green algae (Table 4) can also be common colonizers.These algae supply limited amounts of nutrients to the sediment (Williams, 1990) but have minimum sediment binding capability (Zieman, 1982). In the Western Atlantic, the pioneer seagrass species is *Halodule wrightii*, which either colonizes from seed or through rapid vegetative spreading of nearby plants, thereby further stabilizing the sediment surface. In some sequences of succession, *Syringodium filiforme* appears instead of *H. wrightii* (Williams, 1990), or *S. filiforme* colonizes after the latter species, in which case the two species grow intermixed. *S. filiforme* is the least constant member in the sequence of succession and is frequently absent. With time and increasing development of the community, *T. testudinum* colonizes the region (Zieman, 1982; Williams, 1990). Its dense leaf canopy and rhizome and root system efficiently trap and retain particles, increasing the organic matter of the sediment and fueling the sedimentary microbial cycles. Williams (1990) experimentally removed all vegetation from 1 m^2 plots and found that *T. testudinum,* after slightly more than 1 year, reached a critical density ($\sim$200 foliar shoots m^{-2}), at which it exerted control over the sedimentary nitrogen cycle. At this critical density of *T. testudinum*, numbers of rhizophytic algae and *S. filiforme* in the experimental plots declined (Williams, 1990), but she found that *T. testudinum* density and ammonium production rates in the sediments were still lower in her experimental plots than in the undisturbed controls at the end of the experiment (after 52 months). She suggested that *T. testudinum* is an atypical climax species in that is has a relatively high nutrient demands and a high (leaf) growth rate (see also Duarte and Chisano, 199). But rhizome elongation rates of *T. testudinum* are comparatively low. Gallegos et al. (1994) reported rhizome elongation rates of 51.6 and 80.9 cm year^{-1} per apex for the seagrasses *S. filiforme* and *H. wrightii* respectively, which are considerably higher than the rates of 19–35 cm year^{-1} per apex reported for *T. testudinum* (see section 4.1). Fourqurean et al. (1992) showed that *H. wrightii* had a four-fold higher demand for phosphorus (which is the limiting nutrient in carbonate sediments) than *T. testudinum*. A consequence of this high nutrient demand of *H. wrightii* is that after the continuous supply of external nutrients, retrograde succession occurs, resulting in a community with dominance of the early colonizer *H. wrightii* (Fourqurean et al., 1995: see section 6.2). Williams (1990) in her study of secondary succession in the experimentally denuded plots in a reef lagoon at the US Virgin Islands, found that when the community advanced toward its climax state, co-existence rather than replacement of species occurred. She suggested that co-existence of more species in a *T. testudinum* community in the Caribbean could be attributed to niche partitioning (mainly caused by different rooting depths and differential nutrient demand of the species) or to increasing resource supply (nutrient accumulation) as succession progresses, in accordance with the resource-ratio model of Tilman (1985). But Clarke and Kirkman (1989) and Duarte et al. (1997a), suggested that (intermediate) perturbations were of primary importance in maintaining multispecific seagrass meadows in the Indo-Pacific.

In the Indo-Pacific, *T. hemprichii* often occurs intermixed with various seagrass species (Table 4, see section 6.1), and colonization sequences of cleared areas are closely related to the rate of rhizome expansion of each species. Rollon et al. (1998) experimentally denuded plots in a mixed seagrass meadow in the Philippines and observed that *Halophila ovalis* was the most conspicuous early colonizer, reaching high density within half a year after disturbance. But invasion of larger species such as *Cymodocea rotundata*, *Syringodium isoetifolium*, and *Halodule univervis* reduced the *H. ovalis* densities to pre-disturbance levels. The naturally-dominant species *T. hemprichii* and *Enhalus acoroides* were the last to colonize, the first reaching pre-disturbance levels after 2 years, whereas the latter required a little less than 10 years for full recovery. Some early species colonized from seeds, but in general, rhizome expansion of plants in nearby meadows was most important. The sequence of succession reported by Rollon et al. (1998) was in accordance with the rhizome expansion rates reported by Vermaat et al. (1995) for these species in a mixed seagrass meadow, where they found highest expansion rates for the early colonizers such as *H. ovalis* (141.0 cm year^{-1} apex^{-1}), lowest rates for the climax species *T. hemprichii* and *Enhalus acoroides* (at 20.6 and 5.3 cm year^{-1} apex^{-1}, respectively) and intermediate rates for the species *S. isoetifolium* (134.7 cm year^{-1} apex^{-1}), *C. serrulata* (78.3 cm year^{-1} apex^{-1}), *C. rotundata* (33.9 cm year^{-1} apex^{-1}), and *H. uninervis* (28.4 cm year^{-1} apex^{-1}), which followed *H. ovalis* in succession but preceded the climax species. The shoots of the later colonizers attained a greater age and were larger than those of the early arrivers (Vermaat et al., 1995). The sequence of secondary succession after gap formation through experimental burial in a mixed Philippine seagrass meadow was similar to that reported by Rollon et al. (1998), with the exception that the climax species *E. acoroides* was resistant to the burial treatment (Duarte et al., 1997a).

Although the structure of *T. testudinum* and *T. hemprichii* communities may vary considerably, mainly because *T. hemprichii* meadows contain more seagrass species, general patterns in structural changes and processes during succession are similar. With the progression toward a climax community, there is an increase in the belowground biomass of the community as well as the leaf portion exposed in the water column, and more nutrients are sequestered by the seagrasses (Fig. 2). The increase in leaf area provides an increase in surface area for colonization by epiphytic algae and fauna, with the surface area of the climax community being many times that of either the pioneer seagrasses or the initial algal colonizers. In addition to providing a substrate, the larger leaf area also increases leaf-baffling and sediment-trapping effects. Thus, as the canopy component increases, so does newly deposited material in the sediment. The climax species *T. testudinum* and *T. hemprichii* (with also *E. acoroides* in the Indo-Pacific), have the highest leaf area, the highest total biomass, and by far the greatest amount of material in the sediments of any species dominant in the earlier stages of succession (Fig. 2).

D. Faunal Assemblages

Thalassia meadows contain a wide range of benthic, demersal, and pelagic organisms that are either permanent residents of the system or transients. The transient species are frequently juvenile stages of numerous organisms that seek food and shelter during critical parts of their life cycles, or they may be daily visitors that use the *Thalassia* meadows as feeding grounds. The wealth of literature on fauna in seagrass systems indicates that the faunal assemblages of seagrass meadows are not specific, but largely comprise species occurring outside the seagrass meadows as well. The abundance and diversity of fauna associated with *Thalassia* meadows (as with other seagrasses) is high compared with that of unvegetated areas (Hemminga and Duarte, 2000a). Sanchez (1997), for example, reported densities of pink shrimp (*Penaeus duorarum*) in the Gulf of Mexico to be on average 13 times greater in *Thalassia testudinum* meadows than on nearby unvegetated soft substrata.

Thalassia meadows play a key role for fauna in a number of ways. They serve as a feeding habitat by offering food in the form of fresh seagrass tissue, epiphytes, detritus, or associated fauna (Greenway, 1995; Schwamborn and Criales, 2000; Sluka and Miller, 2001; Kirsch et al., 2002). Recent reports suggest that the importance of leaf herbivory in seagrass meadows is often seriously under-estimated (Valentine and Heck, 1991; Cebrian and Duarte, 1998; Valentine and Heck, 1999), and highly variable among seagrass species (Cebrian et al., 1998). Few studies have considered the possibility that herbivores may stimulate rates of primary production, or the role of belowground nutrient reserves in determining the impacts of grazers on seagrasses (Valentine and Heck, 1999; Stapel and Erftemeijer, 2000). The meadows also supply a substrate for settlement for bivalve spat (Bologna and Heck, 2000), juvenile sea cucumbers (Mercier et al., 2000) or epiphytic hydroids and foraminifers (Kaehler and Hughes, 1992; Fujita and Hallock, 1999). The importance of *Thalassia* meadows as nursery grounds for fishes and crustaceans is well documented (Aliaume et al., 1993; Erftemeijer and Allen, 1993; Arrivillaga and Baltz, 1999; Thayer et al., 1999; Nagelkerken et al., 2000; Spitzer et al., 2000). One of the factors underlying the attractiveness of *Thalassia* meadows to juvenile fishes, shrimps, and other fauna is the provision of shelter by the seagrass canopy, which significantly reduces vulnerability to predation (Ray and Stoner, 1995; Jordan et al., 1997; Rooker et al., 1998; Peterson et al., 2001).

The associated fauna, in turn, influence *Thalassia* growth through herbivory on the seagrass tissue (Valentine et al., 1997; Sluka and Miller, 2001), leaf burrowing (van Tussenbroek and Brearley, 1998), epiphyte grazing (Gacia et al., 1999; Heck et al., 2000), and fragmentation of detritus (Lawson et al., 1993; Stoner et al., 1995). Associated fauna may also affect nutrient cycling, substrate stability, and water quality in *Thalassia* meadows through bioturbation (Valentine et al., 1994; Stapel and Erftemeijer, 2000), and suspension feeding (Peterson and Heck, 1999, 2001; Prager and Halley, 1999).

The echinoderm fauna is some of the most conspicuous component of *Thalassia* seagrass communities. Sea urchins (Echinoids) comprise the main grazers in the *Thalassia* ecosystem. Folivory by the sea urchin *Lytechinus variegatus* increases the shoot density and productivity of *Thalassia testudinum* in Florida, and controls its seasonal changes in abundance (Valentine et al., 1997, 2000). Sea urchin grazing in enclosures dramatically affected seagrass habitat structure for long periods of time (>3.5 year). Intermittent grazing produced significant reductions in aboveground plant biomass compared to controls, while continuous grazing produced apparently permanent loss of seagrasses (Heck and Valentine, 1995). In contrast to findings reported for vertebrate herbivores, sea urchins were found to feed at higher rates when offered *Thalassia* leaves of lower nitrogen content, compensating for the lower nitrogen levels by eating more leaves than in treatments where leaf nitrogen was experimentally elevated using commercial fertilizer (Valentine and Heck, 2001). This demonstrates that low levels of leaf nitrogen are not always an effective defense against herbivores. A demographic study of *L. variegatus* in the Gulf of Mexico revealed a catastrophic mortality caused by a cold front in the spring of 1993, leading to a dramatic decline in sea urchin densities in a *Thalassia testudinum* meadow. After a pronounced recruitment event in the fall of 1993, the population at this site recovered within a period of approximately 6 months, which was attributed to the immigration of new adults (Beddingfield and McClintock, 2000). In Indonesia, the edible sea urchin *Tripneustes gratilla* was observed to prefer grazing on attached fronds of *Thalassia hemprichii,* foraging continually throughout the day and night, without evidence of any periodicity (Klumpp et al., 1993). *T. gratilla* consumed only 1–5% of *Thalassia* production between March and July, while between November and March the sea urchin consumption increased to over 50% of seagrass production. They concluded that on an annual basis, *T. gratilla* consumes about 24% of total seagrass production. Experimental reduction of the abundance of *Echinothrix diadema* sea urchins in *Thalassia hemprichii* meadows in a Kenyan coral reef lagoon protected from fishing led to increased bite rates on herbivory assays by parrotfishes, implying that sea urchins can reduce grazing rates of some species of parrotfishes (McClanahan et al., 1994).

Amongst the most important values of *Thalassia*-dominated seagrass meadows are their effects on the fauna associated with these meadows. These seagrass meadows serve as a nursery ground and habitat for fishes, crustaceans, echinoderms, and molluscs of economic importance, thereby sustaining local fishing economies and their food supply. They are also rich in biodiversity (Arrivillaga and Baltz, 1999; Prieto et al., 2000; Gell and Whittington, 2002) and function as critical habitat and feeding grounds for endangered species, such as the green turtle (Greenway, 1976; Williams, 1988), West Indian manatee (Marshall et al., 2000) and dugong (de Iongh et al., 1995; Preen, 1995), thus qualifying as priority areas for conservation.

IX. Conclusions

During the last decade, the rapid increase in seagrass studies (see section 1.3) has continued, as is indicated by the multitude of recent references cited in the present work. But it is striking that most research on tropical seagrasses, and *Thalassia* in particular, has been mainly realized in first world territories or conducted by first-world visiting scientists to tropical territories. There exists a major need to involve scientists from tropical Western Atlantic and the Indo-Pacific in basic seagrass research. This need is even more urgent in light of the decline of many tropical seagrass communities due to rapid increases in exploitation and urbanization of the many tropical coasts, particularly in South-East Asia and the Caribbean (Green and Short, 2003). The huge extent of *Thalassia* beds may give a false impression of community resistance to the rapidly changing conditions in these coastal areas. Yet our knowledge concerning the foundations of these communities in still insufficient, and basic research into the processes and interactions, which permit seagrasses to cover huge coastal areas, are essential for conservation.

Eutrophication of coastal waters caused by human development may locally be an important nutrient input in *Thalassia* meadows (Touchette and Burkholder, 2000), and it is likely that human-induced eutrophication poses a serious threat to *Thalassia* meadows (Wear et al., 1999). *T. testudinum* biomass and productivity are negatively correlated with watershed nitrogen loads (Tomasko and Lapointe, 1991; Tomasko et al., 1996), which cause a decline in both the percentage cover and aboveground biomass (McGlathery, 1995). In enriched beds, primary production rates, biomass, and chlorophyll-a content of epiphytes were significantly greater than in control beds (Wear et al., 1999), resulting in reduction of available light (Peterson and Heck, 2001), thereby negatively affecting the seagrasses, which are vulnerable to light reduction (Hemminga, 1998) and smothering by the epiphytes (Orth and van Montfrans, 1984). Human-induced nutrient addition may also result in changes in the species composition of the meadows (e.g. *H. wrightii* replaced *T. testudinum* under high-nutrient conditions: see section 6.2). For plant communities in general, diversity tends to diminish under conditions when growth rates of all competitors are high (Huston, 1979), and knowledge concerning the interactions and competitive displacement capacities of the seagrasses and rooted macroalgae in relatively diverse *Thalassia* meadows in oligotrophic systems are required to timely detect critical changes in these communities.

Colonization and population maintenance of *Thalassia* occur almost exclusively through vegetative spread and branching of the rhizomes. Thus, knowledge of the development and organization of the vegetative structure forms the basis for further understanding how these species cover thousands of square miles of the sea bottom. Yet, since the studies of Tomlinson (see section 4.1), virtually no research has been conducted on the vegetative anatomy and development of *Thalassia*, despite the fact that Tomlinson (1974) himself stressed that many of his observations were based on superficial examination, and that his work was preliminary and incomplete. Studies into the demography of shoots have been a useful tool in understanding some aspects of the dynamics of the shoot (ramet) populations, but information concerning dynamics of the genets such as their vegetative extension and dispersal through sexual propagules is scarce. Also our knowledge on the processes of clonal growth (clonal diversity, sizes of the clones, spacing of clones in a meadow, consequences of clonal growth in acquisition of resources) is also limited. An important reason for this our limited knowledge of population dynamics (at a higher level than the shoots) and clonal biology are the high degree of entanglement of rhizomes that makes it logistically almost impossible to tell individuals other than the ramets (shoots) apart. It is hoped that with the coming of high-resolution genetic markers will greatly increasing our insights in this field.

Human development of the coastal zones not only causes a decrease in total extend of seagrass meadows, but also cause fragmentation of these naturally extensive seagrass beds, and the formation of edges and remnant patches through fragmentation is considered to be critical in terms of conservation (Wilcox and Murphy, 1985). Fragmentation of beds is thought to cause impoverishment of faunal diversity and distribution, although Bell et al. (2002) found few differences between areas with and without boat propeller scars. Uhrin and Holmqvist (2003), on the contrary, reported lower faunal abundance and species richness in areas denuded of seagrasses by propellers. Habitat fragmentation may also have consequences for nutrient retention. There are clear indications that in oligotrophic areas, nutrient conservation for *Thalassia* depends on the meadow as a whole (section 3), thus division into smaller patches may have serious consequences for the persistence of this genus in these environments. On a larger scale, habitat fragmentation may increase genetic drift in isolated populations, resulting in a decrease in genetic diversity, but knowledge concerning genetic diversity of *Thalassia* is just emerging, and little is known about their capacity of dispersal and (re-)colonization of distant perturbed areas. Future research into these and other basic aspects of seagrass biology are urgently required before more seagrass habitat is lost along the tropical coasts of the Atlantic and Indo-Pacific.

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Chapter 19

Epiphytes of Seagrasses

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I. Introduction

In all aquatic environments, available surfaces are rapidly colonized by a variety of organisms. If these organisms grow on plants they are called epiphytes. Seagrasses provide an excellent substratum for epiphytic organisms and these organisms are an integral component of seagrass ecosystems. The ecology and physiology of seagrass epiphytes have been reviewed previously (Harlin, 1980; Borowitzka and Lethbridge, 1989) and this chapter focuses primarily on new developments in our understanding of seagrass epiphyte[1] biology and ecology that have occurred since then.

Seagrasses grow in a wide range of habitats ranging from the intertidal to depths of over 50 m (Long et al., 1996), from estuarine to marine environments, and from temperate regions to the tropics. The different seagrass genera also show a diversity of morphologies ranging from the simple subulate leaves of *Syringodium* and the strap-shaped leaves of *Cymodocea*, *Posidonia*, *Thalassia*, and *Zostera*, to species with upright lignified stems with terminal strap-shaped leaf bundles as in *Amphibolis*, providing a structurally diverse range of habitats (refer to Kuo and den Hartog, Chapter 3, for further details). The above-ground parts of seagrasses provide a temporary, but continuously renewing, substratum for epiphytic organisms. The life-span of the leaves, stems, and rhizomes upon which epiphytic organisms can grow varies between species, habitats and with season and ranges from about 11 days for *Halophila ovalis* leaves to about 130 days for *Posidonia* leaves and over 2 years for stems of *Amphibolis antarctica* (Fig. 1).

II. The Role of the Epiphytic Organisms

A. Primary Producers

The epiphytic algae of seagrasses are important primary producers in seagrass ecosystems and make a significant contribution to food webs. They can account for over 50% of the standing stock in seagrass meadows. In Florida, USA, epiphytic algae contributed 62, 50, and 44% of primary production for *Syringodium filiforme*, *Thalassia testudinum,* and *Halodule wrightii*, respectively (Wear et al., 1999). In Papua New Guinea, Heijs (1984) determined that the epiphytic algae on *T. hemprichii* contribute

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[1] The term *epiphyte* is variously defined in the literature. In this chapter, we define an *epiphyte* as an organism that grows upon plants. *Periphyton* are the microalgae (diatoms, dinoflagellates, juvenile germlings of larger algae, etc.), bacteria, protozoa, etc. on surfaces such as seagrass leaves.

A. W. D. Larkum et al. (eds.), Seagrasses: Biology, Ecology and Conservation, pp. 441–461.

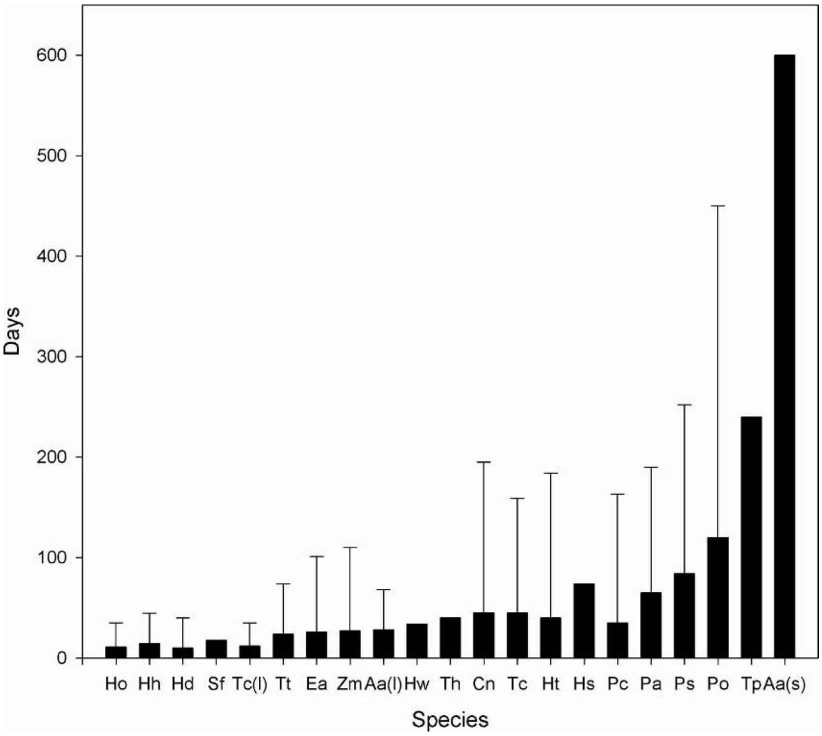

Fig. 1. Minimum and maximum life of seagrass leaves. Separate data for leaves and stems are indicated by (l) and (s), respectively. Aa = *Amphibolis antarctica* (Walker, 1985); Cn = *Cymodocea nodosa* (Reyes et al., 1998); Ea = *Enhalus acaroides* (Johnstone, 1979; Brouns and Heijs, 1986); Ho = *Halophila ovalis* (Hillman, 1987); Hh = *H. hawaiiana* (Herbert, 1986); Hd = *H. decipiens* (Josselyn et al., 1986); Hs = *H. stipulacea* (Wahbeh, 1984); Hw = *Halodule wrightii* (Morgan and Kitting, 1984); Ht = *Heterozostera tasmanica* (Bulthuis and Woelkerling, 1983b); Pa = *Posidonia australis* (West and Larkum, 1979; Silberstein et al., 1986); Pc = *P. coriacea* (Lavery et al., 1999); Po = *P. oceanica* (Ott, 1980; Zupo et al., 1997); Ps = *P. sinuosa* (Walker, 1977; Jernakoff and Nielsen, 1997); Sf = *Syringodium filiforme* (Zieman et al., 1979); Th = *Thalassia hemprichii* (Heijs, 1984); Tt = *T. testudinum* (Patriquin, 1973; Zieman et al., 1979); Tc = *Thalassodendron ciliatum*; Zm = *Zostera marina* (Sfriso and Ghetti, 1998).

from 19 to 37% of the total primary production and Silberstein et al. (1986) showed that >60% of the total maximum photosynthetic rate of *Posidonia australis* in Cockburn Sound, Western Australia, could be attributed to epiphyte photosynthesis. On the other hand, Brouns and Heijs (1986) estimated that only 2–9% of the total annual mean above-ground production of *Enhalus acaroides* was produced by the epiphytic algae.

B. Sediment Formers

Calcareous red algae are common epiphytes of seagrasses and these contribute to the production of calcareous sediments. Land (1970) produced the first estimate of epiphytic carbonate production and since then there have been several other studies. Estimates range from 1.9 to 282.7 g $CaCO_3$ m^{-2} $year^{-1}$ for *T. testudinum* beds in Florida Bay, USA, and these values are equivalent to the carbonate sediment production by other calcareous organisms in this region such as molluscs and the calcareous algae *Halimeda* and *Penicillus* (Frankovich and Zieman, 1994). Even higher rates have been reported for *T. testudinum* epiphytes in Barbados (2800 g $CaCO_3$ m^{-2} $year^{-1}$; Patriquin, 1972), and for *A. antarctica* in Shark Bay, Western Australia (50–526 g $CaCO_3$ m^{-2} $year^{-1}$; Walker and Woelkerling, 1988).

C. N_2-Fixation and Nutrient Cycling

Seagrass ecosystems show high levels of N_2-fixation and this has been attributed mainly to bacteria in the rhizosphere (Welsh, 2000) although cyanobacterial epiphytes on the seagrass leaves can also make a significant contribution in some systems

(Goering and Parke, 1972; Iizumi and Yamamuro, 2000; Pereg-Gerk et al., 2002). In most cases, the main N_2-fixing organisms on the leaves are cyanobacteria and it has been estimated that they can supply 4–38% of the nitrogen needed for primary production in *T. testudinum* beds (Capone and Taylor, 1977). This nitrogen may be made available by grazers feeding on the cyanobacteria thus releasing the nitrogen for uptake by the seagrass (Yamamuro, 1999). Pereg et al. (1994) have also suggested that anaerobic photosynthetic bacteria of the Rhodospirillaceae also contribute to N_2-fixation observed on seagrass leaves.

Seagrass epiphytes are also likely to be nutrient 'sinks'. It has been estimated that the epiphytes of *T. testudinum* are responsible for about 17% of the total NH_4^+ removed from the water column by the whole seagrass meadow (Cornelisen and Thomas, 2002). However, little is known of how much epiphytic algae compete with the seagrass for available nutrients and more studies are needed to assess the importance of seagrass epiphytes to nutrient cycling (see Mateo et al., Chapter 7).

III. Distribution and Abundance of Epiphytic Organisms

The epiphytic organisms found on seagrass leaves, stems, and rhizomes generally show distinct patterns in their distribution.

A. Bacteria, Fungi, and Protozoa

Bacteria, fungi, and protozoa are ubiquitous members of the epiphytic community but remain little studied. The bacterial flora of *Zostera marina* has been the object of several studies (Sieburth and Thomas, 1973; Kirchman et al., 1984; Barnabas, 1992). A bacterial film is discernible on new seagrass leaves within 1 h (Novak, 1984) and young leaves of *Z. marina* and *Posidonia oceanica* have a significantly lower bacterial density than older leaves (Kurilenko et al., 2001), with the bacteria most abundant on the leaf tip. On mature leaves this gradient is reversed and bacterial density is highest at the leaf base (Novak, 1984). Wahbeh and Mahasneh (1984) also observed differences in viable counts of heterotrophic bacteria attached to various parts of *Halophila stipulacea*. Maltas and Borowitzka (unpublished results) have also found distinct seasonality in the abundance and diversity of culturable bacteria on the leaves of *P. australis* and *A. antarctica*.

Bacteria found on seagrass leaves include the genera *Vibrio, Alteromonas*, *Moraxella*, *Pseudomonas*, *Marinobacter*, and *Brochothrix* (Maltas and Borowitzka, unpublished, Kurilenko et al., 2001) as well as several nitrogen fixing bacteria (Pereg et al., 1994). New methodologies such as restriction fragment length polymorphism analysis of 16S rRNA genes (Weidner et al., 1996) will provide further important information on the diversity of the prokaryotic epiphytes of seagrasses and their possible roles.

B. Algae

The most abundant and diverse epiphytic organisms on seagrasses are algae. These range from unicellular diatoms and dinoflagellates found on almost all seagrasses (Kita and Harada, 1962; Buia et al., 1996; Jernakoff and Nielsen, 1997; Mazzella, 1999) to large macrophytes such as *Laurencia* spp., *Metagoniolithon stelliferum*, and *Hypnea* spp. found attached to the stems of *Amphibolis* spp. (Lethbridge et al., 1988). Seagrasses are also host to a wide range of other epiphytes including fungi (Belofsky et al., 1999), protozoa (Aladro-Lubel and Martínez-Murillo, 1999; Saraswati, 2002), sponges, bryozoans, hydroids, and ascidians (see later). Furthermore the primary epiphytes may have dease populations of microalgae, such as bacteria and diatoms, and bacteria. Other invertebrates such as crustaceans and molluscs live amongst the sessile epiphytic flora and fauna.

With few exceptions, the diversity and biomass of epiphytic algae is highest on the leaves, especially on the oldest leaf and near the leaf apex (Buia et al., 1985; Cullinane et al., 1985; Borum, 1987; Mazzella et al., 1994; Reyes et al., 1998; Trautman and Borowitzka, 1999; Uku and Bjoerk, 2001). This pattern has been reported for most species with strap-like leaves, including *Z. marina*, *Posidonia sinuosa*, *P. australis, P. oceanica*, *Cymodocea rotundata*, *Thalassodendron ciliatum*, and *Thalassia hemprichii*. A similar apico-basal pattern has also been observed in *Syringodium isoetifolium* (Yamamuro, 1999). Some notable exceptions to these generalizations are species of *Amphibolis* and *Thalassodendron*, and *P. oceanica*. In *Amphibolis*, for example, the majority of epiphytic algae occur on the long-lived stem, with relatively few species and significantly lower biomass on the leaves (Borowitzka et al., 1990; Lavery and Vanderklift, 2002). Interestingly, an apico-basal pattern of epiphyte distribution is not observed on some seaweeds such as *Cystoseira* (Belegratis et al., 1999). The rhizomes of seagrasses generally carry a low epiphyte load compared with the leaves, with the exception of *P. oceanica* where greater species richness and higher biomass on the exposed and long-lived rhizomes has been reported (Piazzi and Cinelli, 2000; Mateo et al., Chapter 7). The low abundance of epiphytes on rhizomes is probably due to the fact that the rhizomes of almost all seagrasses are buried most of the time.

There are few truly comparative studies of the epiphyte assemblages on different seagrasses (but see Pinckney and Micheli, 1998; Trautman and Borowitzka, 1999; Wear et al., 1999; Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). In contrast, there are a large number of studies on the biomass and composition of epiphyte assemblages on single seagrass species, usually related to questions about the effect of environmental factors on these assemblages. Comparisons across species are often, therefore, gleaned from the literature. However, this is fraught with difficulty as the studies are performed over different time scales and, as this chapter will show, time scale is a crucial source of variability in epiphyte assemblages.

While we might expect differences in patterns of distribution between seagrasses with markedly different morphologies, subtle differences in morphology can also have significant effects on epiphyte assemblages. For example, *P. sinuosa* and *P. australis* are morphologically similar seagrasses with strap-like leaves; the leaf of *P. sinuosa* is narrower and is concave in transverse section unlike *P. australis,* which is wider and flat. Trautman and Borowitzka (1999) found that the epiphyte assemblage on *P. sinuosa* leaves differed between the two leaf sides, with greater species richness and biomass on the convex surface, including some species restricted to only that side; no differences in species richness or abundance of epiphytes were noted between adaxial and abaxial sides of leaves of *P. australis*. Similar observations were made in respect to epiphytic invertebrates (see below).

Seagrasses with distinct morphological differentiation tend to provide several distinct microhabitats for epiphytes and there are reports of epiphytic algae that are confined to particular plant parts. In *Amphibolis*, for example, few species of epiphyte are common to both stem and leaf, with most on the stem and some showing specificity to a particular part of the stem (Lethbridge et al., 1988; Borowitzka et al., 1990). This within-plant spatial specificity of epiphytes is not confined to seagrass species with long-lived stems. Cullinane et al. (1985) found a similar pattern on *Z. marina*, except that some taxa were confined to different parts of the leaf/sheath structure. In the Mediterranean, Piazzi and Cinelli (2000) noted distinct leaf and rhizome assemblages on *P. oceanica*, with 28 leaf taxa (dominated by encrusting coralline algae and brown algae species) but 56 species on the rhizome (dominated by filamentous Rhodophyta—*Acrothamnion*, *Womersleyella*, and the crustose *Peyssonnelia*); only 13 taxa were common to both niches. Borowitzka et al. (1990) also observed distinct fine-scale patterns in the distribution of epiphytic algae; on *A. griffithii* leaves, for example, plants of the green alga *Bryopsis plumosa* were usually found only on the leaf tips whereas the rhodophyte *Ceramium puberulum* was most common at the base of the leaves near the leaf junctions. These observations suggest that even small differences in turnover rates of plant parts as well as localized variation in hydrodynamics can provide sufficient habitat differentiation to result in distinct epiphytic algal assemblages.

The composition of the assemblages of epiphytic algae includes taxa from all the major algal phyla. Generally, red algae dominate the composition and biomass and diatoms are almost ubiquitous. This dominance by rhodophytes reflects the dominance of this phylum in the surrounding environment. Where other phyla dominate the seagrass epiphyte flora, there is an implication of unusual environmental conditions, such as nutrient enrichment resulting in an abundance of green algae or cyanobacteria (Coleman and Burkholder, 1994; Ierodiaconou and Laurenson, 2002) or changes in energy levels and depth resulting in shifts between diatoms and cyanobacteria (Pinckney and Micheli, 1998). Consequently, most reports of cyanobacterial or green algal domination suggest these are either transient, or regular but seasonal, events coinciding with seasonal nutrient inputs. Alternatively, they are from estuarine seagrass habitats.

The number of species of epiphytic algae found on different seagrass species varies considerably. It should be noted, however, that most studies of the algal epiphytes of seagrasses focus only on the

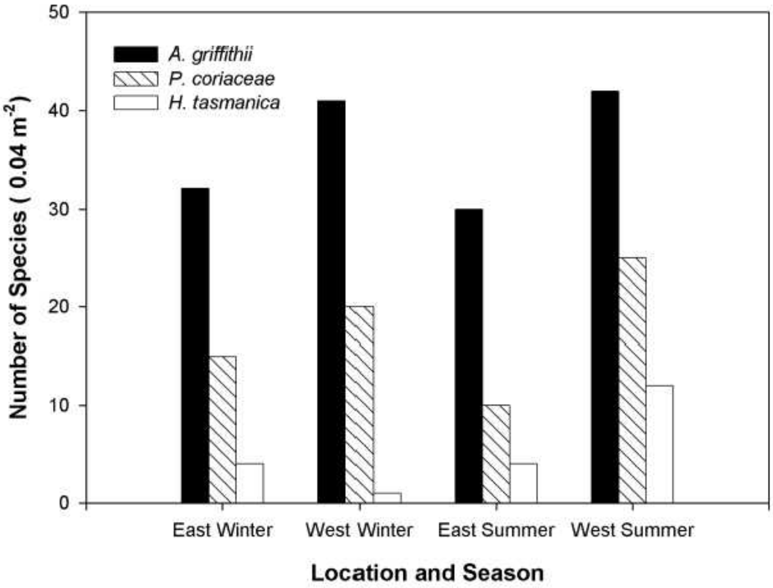

Fig. 2. The mean number of epiphytic algal species present on three seagrasses of differing structural complexity and longevity (*Amphibolis griffithii*, *Posidonia coriacea,* and *Heterozostera tasmanica*) located in the same general location off Perth, Western Australia, at two sites (east and west) and at the same sampling times. Data are means of six 0.04 m^2 quadrats (unpublished data).

multicellular algae and not the unicells forming part of the periphyton. Unfortunately, there are almost no studies of the diversity and community dynamics of the algal component of the periphyton. However, as Jernakoff and Nielsen (1997) have shown, this community can be very diverse. They found a total of 70 taxa on the leaves of *P. sinuosa* consisting of 62 diatoms, 4 cyanobacteria, 2 dinoflagellates, 1 green alga, and a coralline red alga germling. Similarly, Mazzella et al. (1994) have observed a total of 56 species of diatoms, especially members of the Naviculariaceae, on leaves of *P. oceanica* in the Gulf of Naples.

As a very general rule, the more persistent and structurally complex seagrass species tend to have a greater epiphyte biomass as well as more diverse epiphyte assemblages. However, this generalization is based on a range of studies in different locations and over different time scales, so that the very rich assemblages tend to be recorded over more than one annual cycle. At any one point in time, there are considerably fewer taxa present on the seagrass. For example, Borowitzka et al. (1990) recorded over 150 species of epiphytic macroalgae on *A. griffithii* over the 4 year length of their study at several sites in Western Australia, but only up to 47 species at any one time and place. Where seagrass species occur in the same region, it is generally accepted that short-lived seagrass species are likely to be relatively depauperate in epiphyte species richness and biomass compared to persistent seagrass species. For example, *A. griffithii* (highly persistent), *P. coriacea* (persistent), and *Heterozostera tasmanica* (short-lived) co-occur on sand banks in SW Australia and have been found to support about 90, 60, and 34 species, respectively, over an annual cycle. This same pattern is observed at any one sampling time and sampling region and is even maintained where *P. coriacea* and *H. tasmanica* co-exist in mixed meadows (Fig. 2). Rindi et al. (1999) found 20 species of algae epiphytic on *H. stipulacea* leaves in the Mediterranean and considered this 'remarkably' scarce compared to *P. oceanica* which has been reported as having up to 90 epiphytic taxa. However, Rindi et al.'s (1999) study was a single sampling occasion and they note that *P. oceanica* sampled at the same time and over a similar depth range (but at different location) yielded only 38 taxa, comparable to *H. stipulacea*. Alongi et al. (1993), on the other hand, recorded 30 species of epiphytic algae on *H. stipulacea* at a different site in winter. This suggests that while generic models relating epiphyte diversity to seagrass persistence may hold overall, many other site-specific and seasonal factors interact to confound this relationship.

A few studies have assessed macroalgal epiphytes at the functional group level, using Littler

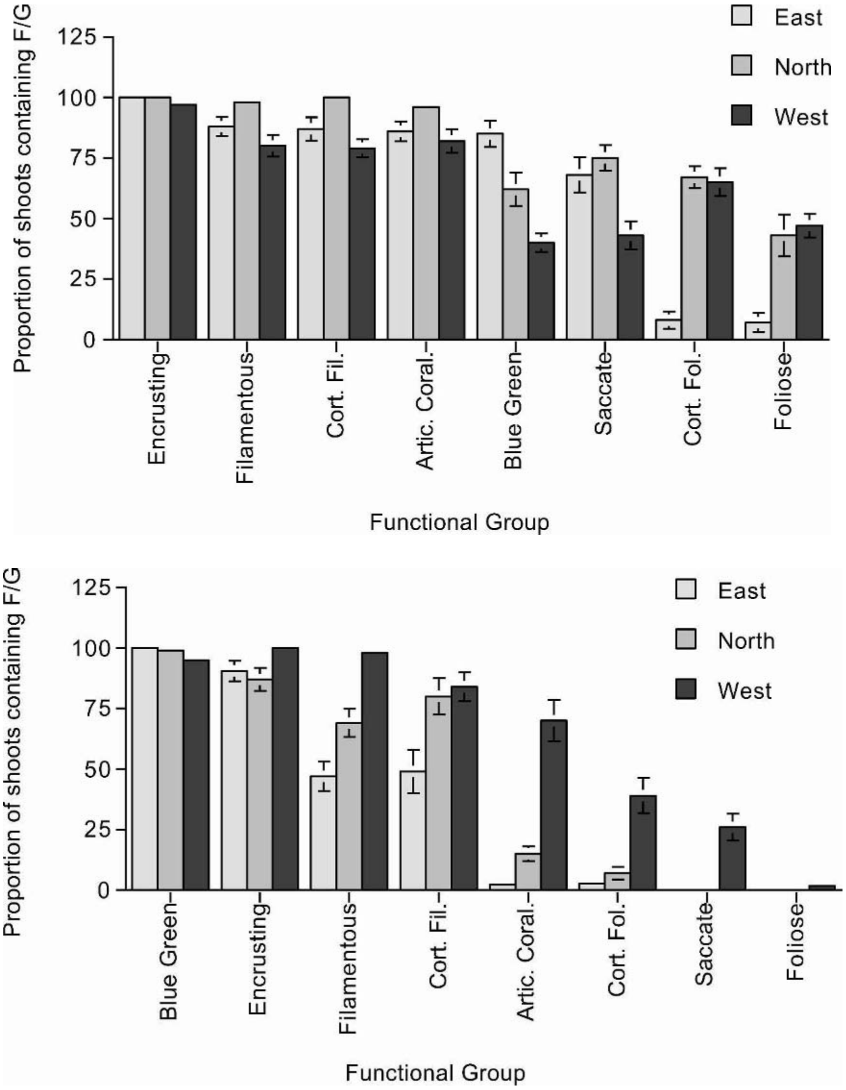

Fig. 3. The proportion of shoots of *Amphibolis griffithii* (top) and *Posidonia coriacea* (bottom) on which different functional groups of epiphytic macroalgae were observed in three different regions separated by 2–3 km (east, west, and north) off Perth, Western Australia. (Data are means ± s.d., $n = 6$).

and Littler's (1980) functional groupings. The number of studies is too limited to allow generalizations to be drawn. These studies also do not test which specific functions are of importance making generalizations difficult (cf. Padilla and Allen, 2000). However, the results suggest that patterns found in distribution and abundance of epiphytic algal species may be paralleled, to some extent, in functional groupings, suggesting that the spatial and temporal patterns in epiphytes species assemblages may have functional implications. For example, Saunders et al. (2003) showed that filamentous, corticated filamentous, and coralline functional groups accounted for 99% of epiphyte biomass on *Z. marina*, but that there were significant differences in the abundances of these functional groups among different seagrass beds. Lavery and Vanderklift (2002; and Fig. 3) have compared the functional grouping of epiphytes on two morphologically distinct seagrasses *A. griffithii* and *P. coriacea*. While there were significant differences in the species composition and abundance of epiphytes on the two seagrasses, each supported assemblages that contained a wide range of functional groups. Further, there were distinct regional differences in the abundance of different functional groups, and these patterns mimicked species-level patterns.

Similarly, Bandeira (2002) showed significant between-site differences in the assemblages of epiphytes on *Thalassodendron ciliatum* stems; in this case only articulated coralline algae occurred at a sandy site but elsewhere articulated coralline, encrusting, corticated filamentous, corticated foliose, and leathery algae were present.

Few studies have examined the variability in composition of epiphytes across spatial scales larger than within plants, despite recognition that the spatial scale is likely to influence the difference between assemblages (Fonseca, 1996). Most information on larger-scale spatial variability has been obtained incidentally, while studying the effects of nutrients or other environmental factors (e.g. Frankovich and Fourquean, 1997; Kendrick and Burt, 1997; Pinckney and Micheli, 1998). However, several recent studies have explicitly examined spatial variation at different scales (Kendrick and Burt, 1997; Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002; Saunders et al., 2003). These studies generally show an increase in dissimilarity of epiphyte assemblages with increasing distance apart. Significant differences occur in assemblages on *P. sinuosa* separated by kilometers on the same shallow coastal bank and across a gradient of wave exposure (Kendrick and Burt, 1997); filamentous browns and reds and cyanobacteria dominated the more inshore site, while articulated and encrusting coralline algae dominated the offshore site. Further, within the filamentous rhodophytes that occurred at each site there were differences; the inshore site was dominated by Rhodomelaceae and the offshore site by Ceramiaceae. Frankovich and Fourqurean (1997) examined epiphyte assemblages across a nutrient gradient and found compositional shifts, though these tended to occur rapidly and close to the nutrient source. Bandeira (2002) also observed a great difference in epiphytes in *Thalassodendron ciliatum* growing on either rocky substrata or sandy substrata at Ithaca Island, Mozambique. He found that the communities at the rocky sites had a diverse epiphytic flora, whereas at the sandy site epiphytes were restricted almost completely to the coralline *Jania adhaerens*, growing on the stems of the seagrass.

A small number of studies have attempted to look at spatial patterns in epiphytes that are independent of obvious environmental gradients. Trends across different species appear similar but with some subtle differences. In *Z. marina*, a seagrass of relatively simple structural complexity, epiphyte assemblages showed no differences in composition or abundance at the scales of less than 10 m, but highly significant differences at the kilometer scale (Saunders et al., 2003). Similar observations were made by Cullinane et al. (1985) also working on *Z. marina*; differences in composition were found at the scale of tens of kilometers, with only one species common to six sites separated at this scale. The composition of epiphytes has also been examined on the structurally complex seagrasses *Amphibolis griffithii* and *Posidonia coriacea* at scales of tens, hundreds, and thousands of meters (Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002). As with *Z. marina*, there were no differences at very small scales (1 m or less) but, in contrast, differences were apparent at scales as low as one to tens of meters. In *P. coriacea*, where leaf turnover is in the order of 50–100 days, there was a linear increase in dissimilarity of assemblages with distance apart but in *A. griffithii*, with long-lived stems up to 2 years old, the differences in assemblages increased almost exponentially with increasing distance apart. This was attributed to interactions of seagrass and algal life-history timescales. These studies of structurally diverse seagrass species indicate that assemblage structure of epiphytes are likely to be variable between sites separated by as little as tens of meters and that these differences will be more pronounced as the spatial scale increases. Furthermore, it appears that these differences hold not only at species level but also at the functional group level (Vanderklift and Lavery, 2000; Saunders et al., 2003; Fig. 3). This implies that the differences have the potential to affect the ecological function of the epiphyte assemblages, and therefore the functional attributes of the seagrass habitats separated at these scales.

Epiphyte community structure and biomass also vary over depth for a wide range of seagrasses. Meadows of the Mediterranean seagrass *P. oceanica* supported a more diverse assemblage at shallow sites, but by 30 m depth there were no epiphytic algae. The relative abundance of rhodophytes increased with depth while phaeophyte abundance decreased (Cinelli et al., 1984; Lepoint et al., 1999). These observations both confirm and contrast those of Rindi et al. (1999) who compared the epiphyte composition of the short-lived Mediterranean seagrass *Halophila stipulacea* at shallow (5 m) and deep

Table 1. Relationship between epiphyte biomass and the phenology of the seagrass.

Species	Functional group	Epiphyte biomass ($g\ m^{-2}$)	Epiphyte biomass ($g\ g^{-1}$)	% of above-ground biomass
Western Australia (Lavery, unpublished results)				
Amphibolis griffithii	Persistent; Structurally complex; Slow stem turnover	50–450	0.56	36
Posidonia coriacea	Persistent; Structurally simple; Slow leaf turnover	1–45	0.16	14
Heterozostera tasmanica	Short-lived; Structurally simple; Rapid turnover	0.1–8	0.02	2.3
Florida, USA (Wear et al., 1999)				
Thalassia testudinum	Persistent; Structurally complex; Slow stem turnover	40–125	0.44	31
Syringodium filiforme	Intermediate persistence and turnover; Structurally simple	60–100	0.58	37
Halodule wrightii	Short-lived; Structurally simple; Fast turnover	20–110	0.78	44

(15–25 m) sites and also found compositional shifts over depth. Shifts in composition of *Z. marina* and *Halodule wrightii* epiphyte assemblages from diatom to cyanobacteria were attributed partially to depth (Pinckney and Micheli, 1998) and effects of depth were observed for more ephemeral seagrass species (*Heterozostera tasmanica*, *Zostera muelleri*, and *Ruppia megacarpa*) over a shallow depth range (0–2 m). Epiphyte biomass at 0–0.5 and 0.5–1.0 m, and on a m^{-2} basis, was about 70% higher than at 1.0–1.9 m. When normalized to leaf biomass, the trend is even more dramatic since seagrass biomass was higher at depth. However, there did appear to be a depth-by-site interaction in this study, suggesting that effects of depth could be over-ridden by other factors.

There are few truly comparative studies of epiphytic algal biomass. Two specific comparative studies have been undertaken, comparing seagrass species with differing morphologies and timescales of persistence (Table 1). One of these compared *A. griffithii*, *P. coriacea*, and *H. tasmanica* which co-occur in Western Australia. Epiphyte biomass in the three seagrasses was highly variable, but was clearly greater in the more persistent and complex species *A. griffithii*, both on an area basis and per gram of seagrass. In another study, Wear et al. (1999) sampled *Thalassia testudinum*, *Syringodium filiforme*, and *H. wrightii*, which also cover a range of seagrass functional types from structurally complex and persistent to simple and ephemeral. In this case, total biomass, expressed per m^2 was comparable on an areal basis, but normalized to seagrass biomass showed the opposite trend to that observed in the Australian study, with the simpler and ephemeral species, *H. wrightii*, having the greater biomass per gram of seagrass. On the basis of these two data sets, it is clear that relative epiphyte biomass does not seem to follow a predictable pattern between seagrass species.

Epiphytic algae have been shown to contribute to more than 30% of the total above-ground biomass in many seagrass ecosystems (Table 2). Published biomass data must, however, be interpreted with some caution; some authors determine total biomass (dry weight) that includes the $CaCO_3$ of the calcareous epiphytes rather than ash-free dry weight and this inflates the overall biomass figure. The $CaCO_3$ of the coralline algae can account for 40–60% of the total dry weight (Borowitzka et al., 1990; Bandeira, 1997). Epiphyte biomass often represents a significant proportion of the primary producer biomass and it is generally accepted that the epiphytic material is more likely to be consumed by grazers and detritivores than seagrass material.

C. Invertebrates

In comparison to epiphytic macroalgae, there are markedly fewer studies of the distribution and abundance of epiphytic macroinvertebrates. Unlike algal

Table 2. Contribution of epiphytic algae to total above-ground biomass as a percentage of seagrass + epiphytes in different seagrass meadows.

Seagrass	Range (%)	Source
Posidonia sinuosa	0–16	McMahon et al. (1997)
	10–32	Kirkman and Manning (1993)
Posidonia coriacea	0.3–42	Unpublished
Thalassia hemprichii	29–42	Moncreiff et al. (1992)
	9	Jagtap (1998)
Thalassia testudinum	31–44	Wear et al. (1999)
Amphibolis griffithii	7–75	Unpublished
Amphibolis antarctica	41–47	Kirkman and Manning (1993)
Syringodium isoetifolium	31	Heijs (1985b)
	29–95	Mukai and Ishijima (1995)
Syringodium filiformis	37–41	Wear et al. (1999)
Cymodocea rotundata	44	Heijs (1985b)
Cymodocea serrulata	53	Heijs (1985b)
Heterozostera tasmanica	0–8.2	Unpublished
Zostera marina	1–36	Moncreiff et al. (1992)
Halodule uninervis	49	Heijs (1985b)
Halodule wrightii	19–68	Moncreiff et al. (1992)
Halodule wrightii	44–52	Wear et al. (1999)
Thalassodendron ciliatum	68.5	Bandeira (2002)
Heterozostera tasmanica/Zostera marina/Ruppia megacarpa	49.5	Ierodiaconou and Laurenson (2002)

epiphytes where there is no clear evidence that any of the algae are obligate seagrass epiphytes, there are several reports of obligate invertebrate epiphytes of seagrasses (e.g. Hughes et al., 1991a). As with epiphytic algae, there are distinct spatial patterns within plants, such as between the stems and leaves on species of *Amphibolis* spp. (Borowitzka et al., 1990; Edgar and Robertson, 1992) and along leaves in other species such as *P. oceanica* (Casola et al., 1987). There is a general inverse relationship between the abundance of epiphytic invertebrates and algae, with the algae more abundant near the plant apex, whereas the invertebrates are most abundant on the lower parts of the plant leaves or stems. Bryozoans, hydroids, and ascidians tend to be more common as epiphytes on seagrasses with long-lived parts, such as *Amphibolis* spp. (Borowitzka et al., 1999) or the rhizomes of *P. oceanica* (Colmenero and Lizaso, 1999). On *P. sinuosa* and *P. australis* leaves, hydrozoans were more abundant on the lower part of leaves, other taxa showed no strong trend in distribution along leaves (species of bryozoa, porifera, and foraminifera) and a of spirorbid polychaete was more abundant near the apex (Trautman and Borowitzka, 1999). A similar distributional pattern was observed on *Z. marina* leaves (Nagle, 1968). In addition, some epiphytic invertebrates, as with algae, showed a preference for the concave side of *P. sinuosa* leaves, including a species of porifera and a hydrozoan. The reasons for these spatial patterns are not clear, but may be related, in some cases, to hydrodynamics around the leaf surface (Trautman and Borowitzka, 1999).

Substratum availability is not the sole determinant of epiphytic invertebrate abundance. The density of tunicates on *Z. marina* is influenced by the particular species of amphipod grazers on seagrasses (Duffy and Harvilicz, 2001). Light availability also has been suggested as a factor negatively influencing the abundance of epiphytic invertebrates. For example, *P. oceanica* assemblages tend to be dominated by epiphytic algae at shallow depth (10 m) but in deeper waters (20–30 m) epiphytic invertebrates dominate, with their contribution to biomass increasing from about one-third to >50% of the total epiphytic biomass (Lepoint et al., 1999).

The motile epifauna has received much more attention than the attached epiphytic invertebrates. Jernakoff et al. (1996) have reviewed the literature comparing the motile epifauna between different types of seagrass and concluded that there were few differences in the composition of motile epiphytic grazers that could be clearly related to the form of the seagrass host, though there were differences in the abundances. Within a species of seagrass host, density of the seagrass does appear to affect motile epifaunal abundance; for example, Edgar and Robertson (1992) noted that more open stands of *Amphibolis* spp. were relatively depauperate in motile epifauna compared with dense stands.

The abundance and distribution of epiphytic macroinvertebrate grazers is strongly influenced by the abundance and distribution of the epiphytic algae or periphyton on which they graze (Bologna and Heck, 1999; Fong et al., 2000; Valentine and Duffy, Chapter 20, Sections V to VIII). The density of grazers is a function of both seagrass habitat structure and the trophic attraction of the habitat. The relative importance of these two factors appears variable, with different studies weighting each factor differently. Artificial seagrass has been used to examine the relative roles of these two factors and showed that heterogeneity of a habitat was not, alone, the major determinant of epiphytic grazer biomass; trophic attractiveness of the habitat appears to be more important (Bologna and Heck, 1999; Boström and Mattila, 1999). However, it seems that different grazers respond to different factors and a comparison of fauna on *A. griffithii* and *P. sinuosa* found that the abundance of amphipod and gastropod grazers correlated with food availability on *P. sinuosa* and with the biomass of leaves on *A. griffithii*, suggesting that in *A. griffithii* provision of cover was more important (Jernakoff and Nielsen, 1998).

IV. Factors Affecting Distribution and Abundance

The observed diversity, distribution, and abundance of epiphytic organisms on seagrasses are the result of the interaction of a number of factors and processes. A fundamental determinant of potential epiphyte diversity is the availability of propagules to colonize any available seagrass substrata. In order to try to understand the settlement of epiphytic algae and invertebrates one also needs to consider some basic aspects of the reproduction of these organisms. The propagules of red and brown algae as well as diatoms are non-motile and are wholly at the mercy of hydrodynamics. On the other hand, the propagules of green algae such as *Ulva* and *Enteromorpha* and the larvae of invertebrates are motile and therefore can be expected to be able to show greater selectivity as to the site of settlement. Actual settling and attachment to this substratum will be dependent mainly on localized hydrodynamics (refer to Koch et al., Chapter 8). Successful recruitment and growth will be a function of light, temperature, nutrients, grazing, and predation as well as other interactions of the organisms with other organisms and their environment. The overall development of the epiphyte community will be limited by the longevity of the seagrass substratum.

A. Succession and Seasonality

The process of colonization of a new seagrass leaf is easily seen by comparing differently aged leaves in a leaf bundle on seagrasses such as *Posidonia*. The earliest colonizers are bacteria and diatoms forming a biofilm, which can be observed on even the youngest leaves (Novak, 1984; Sterrenburg et al., 1995). This is soon followed by a range of algae, especially crustose coralline algae, as well as hydrozoans and bryozoans. In general, organisms once settled and established persist throughout the lifespan of their substratum, the leaf. Settlement is generally greatest at the edge of leaves and near the leaf apex, probably because of the higher turbulence in this region which favors the chance of propagules coming in contact with the leaf surface so that they can attach successfully (Jacobs et al., 1983; Trautman and Borowitzka, 1999). Early studies suggested that certain algae such as *Smithora naiadum* and *M. stelliferum* were host specific to particular seagrasses (e.g. Harlin, 1973; Ducker and Knox, 1978). However, further field observations and studies using artificial seagrasses have shown this not to be the case (Harlin, 1973; Lethbridge et al., 1988). The biofilm which forms on the leaves may, however, be an important factor for the settlement of other organisms, especially invertebrates (Wahl, 1989). The prokaryotic biofilms that are a ubiquitous feature of all surfaces in aquatic environments are complex communities (Stoodley et al., 2002) and this complexity can be seen clearly in published micrographs of seagrass microfilms (e.g. Novak, 1984; Mazzella, 1999). There are many non-seagrass examples showing that marine bacterial and diatom biofilms attract or inhibit settlement and metamorphosis of invertebrate larvae (e.g. Wieczorek and Todd, 1998; Daume et al., 1999; Harder et al., 2002; Steinberg et al., 2002) and the role of such biofilms in structuring the communities of epiphytic invertebrates on seagrass leaves deserves attention.

There appears to be no clear successional pattern in the colonization by macrophytes or invertebrates, rather additional new species recruit to the seagrass over time mainly as a function of propagule availability and local hydrodynamics, leading to increased species richness as the seagrass leaf or stem ages (Bulthuis and Woelkerling, 1983a; Heijs, 1985a,b; Borowitzka et al., 1990). The importance of the availability of propagules is illustrated by the study of Lethbridge et al. (1988) using artificial *Amphibolis*-like seagrasses. They also observed that some algal epiphytes colonized directly by the attachment of larger detached thallus fragments rather than from spores. For example, the hook-like branch tips of the rhodophyte, *Hypnea episcopalis*, entangle with the stems of *Amphibolis* and then form new attachments within a few hours. Similar attachment structures have been observed in *Polysiphonia forfex*, *Dicranema revolutum*, and other algae.

The apico-basal distribution of epiphytic algae observed on the strap-like leaves of seagrasses such as *Posidonia*, *Zostera*, and *Cymodocea* are unlikely to be the result of changes in surface chemistry of the leaves as suggested by Harrison and Durance (1985), but rather are a function of localized differences in turbulence, since exactly the same pattern of settlement is observed on artificial leaves made of plastic tape (Horner, 1987; Trautman and Borowitzka, 1999). Some invertebrates, however, show preferential settlement on to particular parts of the seagrass. For example, the density of newly settled larvae of the spirorbid polychaete *Neodexiospira brasiliensis* were more abundant on the basal part of the leaves of both *Zostera* and *Phyllospadix* (Hamamoto and Mukai, 1999) and this may be the result of a distinct preference for shaded substrata (Saunders and Connell, 2001). On the other hand, the hydroids *Clytia edwardsi* and *Tubularia mesembryantheum* initially settle near the leaf apex of *Z. marina*. *Tubularia* then spread to the lower leaf surface via actinula larvae (Nishihara, 1968). Similarly, the hydroid *Sertularia perpusilla*, an obligate epiphyte of *P. oceanica*, grows downwards on the leaves maximizing the residence time on the leaf and facilitating transfer of hydroids to the short young leaves by stolonization, a method of asexual reproduction (Hughes et al., 1991a,b).

The few long-term studies of seagrass epiphytes show distinct seasonality in both species composition and abundance (e.g. Heijs, 1984; Alcoverro et al., 1997; Reyes et al., 1998; Lepoint et al., 1999; Wear et al., 1999); however, most of these studies are only for a 12-month-period and they therefore provide no information on interannual variation. This seasonality in abundance and diversity appears to be a function of substratum availability (i.e. new seagrass surfaces), substratum stability (i.e. life-time of the seagrass leaf or stem which changes over the year), availability of larvae and propagules of the potential epiphyte, and environmental conditions favoring the growth of the epiphytes. Not surprisingly seagrass epiphytes can be classified into groups based on their seasonal distribution: (a) epiphytes occurring throughout the year, (b) epiphytes with a distinct seasonal pattern in their occurrence, and (c) transient colonizers (Heijs, 1985a). The percent cover and biomass of the epiphytes also shows seasonal variation; however, a distinct pattern is more difficult to determine because the temporal scale of sampling (monthly or quarterly) in many studies is often not well matched to the scale of epiphyte and seagrass leaf turnover.

It has been hypothesized that differences in growth rate of individual seagrass species can account for differences in the spatial patterns of epiphyte diversity. A comparison of *A. griffithii* and *P. coriacea* revealed different relationships between epiphyte diversity and the distance apart of the seagrass meadows (Lavery and Vanderklift, 2002). In *A. griffithii* meadows, there was an almost exponential increase in differences between assemblages as distance between sites increased, whereas in *P. coriacea* meadows differences among samples separated by tens or hundreds meters apart were relatively small. This can be explained in terms of the interaction between the lifespan of the host and the reproductive lifespan of the epiphytes (cf. Reyes and Sansón, 1997). Where the host is long-lived, as for *A. griffithii*, local recruitment from existing epiphytes with fast reproductive strategies can continually reinforce the local composition. While this occurs in *P. coriacea*, its faster rate of leaf turnover results in a reduction in the influence of the local recruitment but an increase in the relative importance of regional recruitment. The result is less dissimilarity among distant *P. coriacea* assemblages compared to *A. griffithii*.

B. The Physical Environment

1. Light and Temperature

Light clearly has a key influence on the distribution and abundance of algal epiphytes. The widely observed apico-basal distribution of epiphytes on seagrasses largely appears to be determined by the light regime: algal epiphytes can out-compete animal epiphytes near the plant apex where there is more light, and vice versa, where there is less light. On a more subtle scale, the distribution on different sides of a leaf as observed in *P. sinuosa* (Trautman and Borowitzka, 1999) may also be determined in part by the light regime, with higher abundances of algal epiphytes recorded on the side that receives more light. On a larger scale, the position of a plant within a meadow or patch can influence the light penetrating the canopy, and hence the epiphyte load observed on it. Edge effects on irradiance penetration into patches of seagrass may play a role in determining epiphyte load and distribution. Carruthers (1994) showed that epiphyte biomass in *Amphibolis* meadows was significantly greater at 50% canopy density than at 100%, suggesting that additional light may play a significant role in determining epiphyte load. However, no edge effects in epiphyte biomass were observed by Saunders et al. (2003) in *Z. marina* beds in Plymouth Sound and this may be a function of the much smaller size and lesser structural complexity of *Zostera* compared to *Amphibolis* as well as the lack of a true, well developed 'canopy', which means that there is no marked light gradient. The effect of light availability on epiphyte abundance can also be seen in studies of seagrass epiphytes over a depth gradient (e.g. Buia et al., 1992; Jagtap, 1998; Lepoint et al., 1999).

Not surprisingly, light intensity affects the growth rate of epiphytic algae (e.g. Lewis et al., 2002); however, epiphyte cover also affects seagrass photosynthesis. Dixon (1999) examined the role of epiphytic growth on attenuating light available to leaves of *T. testudinum* and concluded that epiphyte growth attenuated some 33% of PAR at depth. Drake et al. (2003) also observed that epiphytes did not act merely as neutral density filters, but preferentially absorbed light in the blue and red regions thus competing for photons with the underlying leaves. Gallegos et al. (1991) distinguished PUR (photosynthetically useable radiation) from PAR (photosynthetically available radiation), to emphasize the role of epiphytic growth and phytoplankton in the water column in attenuating particular wavelengths of light available to seagrass leaves (see also Zimmerman, Chapter 13, Section XI). Neckles (1993) examined the spectral influence of the epiphyte matrix on attenuated light and concluded that epiphytic growth attenuated light across a broad spectrum. A recent study by Brush and Nixon (2002) showed that epiphytic algae rapidly attenuated light, but that at higher epiphyte densities this attenuation leveled off to a relatively constant value as the epiphytes floated out from the edges of the seagrass blade. They also observed that red algal epiphytes (e.g. *Polysiphonia* sp.) attenuated light faster than green algal epiphytes (e.g. *Cladophora* sp.) highlighting the importance of the morphology of the epiphytic algae. Encrusting algae such as the coralline algae also reduce light more than erect filamentous species (Bulthuis and Woelkerling, 1983a; Cebrián et al., 1999).

Temperature will also exert a significant effect on the growth of epiphytic organisms and for algal temperature effects would be expected to interact strongly with light availability. There have been no explicit studies of the effect of temperature on seagrass epiphytes; however, there is indirect evidence from seasonal studies which show that epiphyte biomass increases with increasing light and temperature (e.g. Alcoverro et al., 1997; Lepoint et al., 1999; Toyohara et al., 1999). Other factors, such as nutrient availability, however, will interact with these effects. For example, Jacobs et al. (1983) and Borum (1985) demonstrated that epiphytic algal abundance could be either maximal or minimal in summer depending on the degree of nutrient enrichment in the water body.

2. Water Motion

Water motion influences almost every aspect of epiphyte growth (see also Koch et al., Chapter 8). Unfortunately, the study of hydrodynamics as it applies to seagrass epiphyte communities is in a primitive state, and requires considerably more attention. The following outlines some of the major issues.

The supply of propagules of algae and invertebrates is controlled by water motion. The reduction of water flow by seagrass canopies might be expected to assist in the trapping of spores within the seagrass bed; however, very dense canopies may in fact act more as a solid surface, forming an artificial boundary layer and redirecting spores over the top of the canopy. van Keulen (1998) measured apparent increases in water velocity over the surface of seagrass canopies, and postulated this was a form of 'skimming flow'. The structure of seagrass plants has been shown to influence the water velocity profile through the canopy. *Amphibolis* plants have a leafy, dense canopy with relatively bare stems; this permits higher water velocities to penetrate into the sub-canopy region than might be expected for strap-leaved seagrasses, such as *Posidonia* spp. (van Keulen and Borowitzka, 2000, 2002). While the dense growths of epiphytes commonly observed on stems of *Amphibolis* have usually been explained by the long-lived nature of these stems, it is possible that the increased penetration of spores into the sub-canopy layer of *Amphibolis* may also contribute. Ackerman (1986) showed that *Z. marina* plants modified their flow environment to trap pollen during flowering and similar observations have been made for *Amphibolis* (Verduin, 1996). It is likely that morphological roughness also enhances the recruitment of epiphyte spores into the canopy. Many algal spores, by virtue of their small size, may be accommodated within the boundary layer surrounding underwater surfaces (Charters et al., 1973) including seagrass leaves. While this would increase the chances of spore adhesion once within close proximity of the substratum, by permitting the spore to settle in the slower water flow, there would also be some resistance to penetrating the boundary layer as a result of 'skimming flow', whereby ambient water flow is redirected over the top of the boundary layer. Consequently, surface roughness and small-scale turbulence may be important factors in determining final settlement.

Water motion also will influence the supply of food for filter-feeding epiphytes; this may be of particular significance in genera such as *Amphibolis* which have a sparse sub-canopy biomass that permits enhanced penetration of water flow into the meadow.

Rates of nutrient uptake for algae and seagrasses have been shown to be dependent on water velocity in several studies (e.g. Thomas et al., 2000) and Cornelisen and Thomas (2002) have demonstrated that ammonium uptake by the epiphytes of *T. testudinum* increased by an order of magnitude over the range of water velocity (0.02–0.20 m s^{-1}) observed in the field. Water motion may play a role in pumping nutrients out of the sediment, making it available for epiphytes in the canopy (Koch and Huettel, 2000; Koch et al., Chapter 8). Flushing of a meadow will also enhance gas exchange, permitting supply of inorganic carbon (CO_2), and flushing out of waste products (O_2).

Physical damage is a clear result of water motion, and is responsible for clearing old growth out of the canopy at the end of summer. The high wave energies experienced during winter storms also remove excess epiphyte growth that has accumulated during the peak growth periods of summer (unpublished results).

Recently, Schanz et al. (2002) highlighted the possibility for complex physical–chemical–biological interactions affecting epiphyte biomass. They showed in both observational and experimental studies that differences in flow regime can affect epiphyte biomass. Their data are consistent with a 'cascading' effect of water movement that is negatively correlated with grazer abundance and positively correlated with epiphyte abundance. At high flow rates gastropod grazers are dislodged from seagrass leaves and so grazing pressure is reduced, leading, in turn, to higher epiphyte biomass and diversity. The role of enhanced flow rates on nutrient provision to the epiphytes was not explicitly tested, but there is little doubt that a large amount of the response they observed was related to the effect on grazers. Other studies have also reported on the interaction between hydrodynamics and leaf fouling (e.g. Fonseca et al., 1982; Jacobs et al., 1983; Kendrick and Burt, 1997) and together these studies emphasize the need to consider factors other than grazing, habitat complexity, and nutrients as the prime determinants of epiphytic algal assemblages.

3. Nutrients

The common wisdom on the effect of nutrients on seagrasses is that increasing nutrient supply results in the overgrowth of seagrasses by epiphytes and, in extreme cases, the death of the seagrasses (Duarte, 1995; for further discussion see Ralph et al., Chapter 24, Section II A). Fundamental in developing this paradigm have been some early studies (e.g. Orth and Moore, 1983; Cambridge et al., 1986) which have been cited regularly in the literature and repeatedly 'confirmed' with statements that nutrient enrichment stimulated the growth of epiphytic algae (e.g. Wear et al., 1999; Moore and Wetzel, 2000). Observational and experimental studies have, indeed, reported increases in epiphyte biomass in response to nutrient loading (e.g. Silberstein et al., 1986; Tomasko and Lapointe, 1991; Lapointe et al., 1994), while others have demonstrated shifts in composition of epiphytes under nutrient loading (Wear et al., 1999). This has led, implicitly, to the assumption that epiphytes could be a useful indicator of environmental conditions and, in particular, of nutrient concentrations or loads at seagrass sites. However, Lin et al. (1996) found that nutrient addition (NO_3, NH_4, PO_4, either alone or in combination) did not result in greater epiphyte abundance on *Z. marina* in their mesocosms. They argue that this was a result of their mesocosms containing not only various grazers and omnivorous fish, but also almost all plant components (seagrasses, seaweeds, phytoplankton, benthic microalgae, and epiphytes) found in coastal lagoon ecosystems which competed for light, nutrients, and inorganic carbon. These communities respond in a complex manner to nutrient addition, which in turn does not necessarily lead to an increase in the biomass of seagrass epiphytes (see also Valentine and Duffy, Chapter 20). Lin et al. (loc. cit.) did, however, observe changes in species composition. In spring, diatoms were dominant in the controls, PO_4 and NO_3 treatment; whereas green algae and cyanobacteria were dominant in the combined nutrient treatments. In mid-summer the dominant group in the control and PO_4 treatment shifted to green algae, in the NO_3 treatment the shift was to cyanobacteria, and in the combined nutrient treatments diatoms dominated. Seasonal influences on the response of epiphytic algae to nutrient therefore increases appear to be important. For example, increased epiphyte load on *Z. marina* due to high nitrogen loading occurred only in summer at Cape Cod, USA, and coincided with the summer phytoplankton bloom (Hauxwell et al., 2003).

The literature reviewed in this chapter provides ample evidence that epiphyte biomass and/or composition responds significantly to nutrient concentration, grazer abundance, hydrodynamic conditions, depth, and light, and that interactions among these factors make it difficult to deduce the cause of shifts in epiphyte biomass or composition. We also reiterate the earliest observations that it is more likely shifts in both the biomass and the types of epiphytes, not just the biomass, that can result in seagrass loss. This proposition was put forward by authors such as Cambridge et al. (1986) but has become simplified to the paradigm that it is shifts in epiphyte abundance alone that cause seagrass loss.

C. Organismal Interactions

1. Grazing and Predation

Seagrass epiphytes are a food source for a range of grazers and predators and these, in turn, influence the distribution, diversity, and abundance of the epiphytic organisms. Grazers control epiphytic algal biomass in at least two ways: directly through the removal of biomass and indirectly through removal of host substrate. Grazer–epiphyte interactions have been reviewed in detail by Jernakoff et al. (1996). It is abundantly clear from the literature that invertebrate and vertebrate grazers can influence epiphytic algal abundance (Phillipart, 1995; Alcoverro et al., 1997; Fong et al., 2000; Heck et al., 2000; Valentine and Duffy, Chapter 20; Heck and Orth, Chapter 22), with estimates that up to 40% of epiphytic algal production may be lost to grazers (Peduzzi, 1987). The effect of grazing on epiphyte composition is less clear, though recent studies do hint at grazing as a possible structuring force.

Copepods, isopods, and amphipods have been recorded as significant grazers on seagrass epiphytes, especially the periphyton. For example, they reduce the accumulation of epiphytic algae on *Z. marina* (Duffy et al., 2001), and may also influence species composition. In microcosm experiments, Duffy and Harvilicz (2001) showed that seagrass exposed to grazing by the amphipod *Gammarus mucronatus* became overgrown by the red alga *Polysiphonia harveyi* compared to ungrazed controls that became heavily fouled with periphyton and tunicates. In contrast, grazing by the amphithoids *Cymadusa compta* and *Amphithoe longimana* removed virtually all fouling material. Jernakoff and Nielsen (1997) also noted that grazing by amphipods appeared to favor crustose coralline algae over diatoms.

Gastropods consume a wide range of algal epiphytes including the calcareous crustose coralline algae (Padilla, 1985; Nielsen and Lethbridge, 1989) and grazing by gastropods also has been shown to exert a direct control of epiphytic algal biomass on a wide variety of seagrasses and under a range of conditions (Hootsmans and Vermaat, 1985; Phillipart, 1995; Jernakoff and Nielsen, 1997). However, the release of grazing pressure may provide only a temporary increase in epiphytic algal biomass. Controlled experiments showed that the absence of grazers results in dramatic increases of epiphytes on *Zostera* *japonica* but that shortly after the biomass returns to control values (on a per m^2 basis) due to the increased sloughing of leaves, which were (presumed to be) weakened by the epiphytic loads (Fong et al., 2000). This demonstrates the complex interplay of factors, including negative feedback loops that control epiphytic biomass.

Fish grazers have been implicated in direct control of epiphytic algal biomass. The pinfish *Logodon rhomboides* and black mullet *Mugil cephalus* were experimentally shown to reduce epiphyte biomass through grazing, but only at times of the year when the epiphytes were fleshy chlorophytes (Gacia et al., 1999). At other times of the year, when red algae dominate, the exclusion of fish from seagrass plots makes no differences to epiphyte biomass. Elsewhere the same fish species (*L. rhomboides*) was shown to exert a direct control on total epiphyte biomass through grazing (Heck et al., 2000), though this study did not specify the composition of the epiphytic assemblage. Ruiz et al. (2001) also provide evidence that the reduced epiphyte load in *P. oceanica* leaves near fish farms is due to increased grazing.

Grazers can also influence epiphytic algal biomass indirectly through the removal of the seagrass substratum. Urchins can consume 50–90% of *T. testudinum* production (Valentine et al., 1997) and small vertebrate grazers have been shown to remove almost all seagrass production at other *T. testudinum* sites (Kirsch et al., 2002). It may well be that this indirect control mechanism on epiphyte biomass may not be consistent over time, since earlier studies showed that the effect of grazing by urchins on seagrass was highly seasonal (Valentine and Heck, 1991). This indirect control can be so significant that it overcomes nutrient-related effects on epiphytes and can, conceivably, result in indirect control of epiphytes through changes in their host substratum. For example, the presence of grazers in seagrass meadows produced higher densities of short shoots (Valentine et al., 1997). The significance of these sorts of morphological changes for epiphytic algal abundance and distribution is unclear, and is worth investigating as another mechanism by which grazing influences epiphytic assemblages.

Grazers can also influence epiphytic assemblage structure (both species composition and abundance) by selective feeding or by the removal of competitive dominants. Evidence for this has been reviewed by Jernakoff et al. (1996), also van Montfrans et al. (1982) demonstrated the role of selective grazing by a gastropod grazer in the removal of loosely attached diatoms and the subsequent domination by more strongly adhering diatom species. Two other studies suggest that grazing cannot only control the biomass and composition of epiphytic algae, but also seasonality in composition. Fish grazing was shown to control the biomass of algae on *Z. japonica*, but only when the algal assemblage was dominated by green algal epiphytes and not more grazing-resistant red algae (Fong et al., 2000). Nielsen and Lethbridge (1989) showed seasonal differences in the gut content of invertebrate grazers and they explained this in terms of an active preference being demonstrated by grazers rather than a seasonal pattern in food availability. Together, these results indicate a clear ability for grazers to influence not only the composition of epiphytic algal assemblages but also temporal patterns in composition.

A large body of work has clearly demonstrated the potential for ‘top–down’ controls, in the form of macroinvertebrate grazers, to over-ride ‘bottom–up’ controls, such as nutrient enrichment effects, on epiphytic biomass (Valentine and Duffy, Chapter 20; Heck and Orth, Chapter 22). Heck et al. (2000) combined nutrient enrichment and top predator experiments. They noted few significant effects of nutrient additions on epiphyte assemblages but many effects of fish, including a reduction in epiphyte biomass. They attributed this to a combination of direct grazing of epiphytes by the fish and the remaining mesograzers that had avoided predation by the fish. Peterson and Heck (2001) performed a similar experiment, but added mussel surrogates instead of fish. Again, the result was that nutrient additions had little effect on epiphyte biomass but the abundance was reduced in treatments containing the mussel surrogates. This was explained in terms of the surrogates providing structure that afforded protection from predation for the mesograzers and resulted in more intense grazing pressure. These and other results (e.g. Moore and Wetzel, 2000) emphasize that any implied relationships between nutrient enrichment and epiphytic biomass may well be over-simplifications if the role of top–down controls are not also considered.

Filter feeders in seagrass beds can also influence the epiphyte population. For example, Peterson and Heck (2001) found that the presence of the mussel *Modiolus americanus* increased the growth of *T. testudinum* and reduced the epiphyte load on the seagrass leaves. This was attributed to the increased growth rate of the leaves resulting from increased nutrient availability and/or the reduction in the availability of epiphyte propagules due to the filtering of the mussels. Seagrass beds support a high density of filter feeding organisms and preliminary estimates by Lemmens et al. (1996) indicated that the filter-feeders, especially the epiphytic species, associated with *Posidonia* and *Amphibolis* meadows are potentially able to filter the overlying water column daily.

2. Interactions Between Other Biota and Seagrass Epiphytes

The potential exists for interactions between biota other than the epiphyte and host to affect seagrass epiphytes. This has been clearly demonstrated in terms of grazers affecting epiphyte biomass and composition (see above). However, other forms of interaction have been reported including competition between algae and indirect interactions between fauna and epiphytes. Piazzi and Cinelli (2000) described different algal assemblages on the leaves and rhizomes of *Posidonia oceanica* in the western Mediterranean. They found the leaves to support 28 species of macroalgae, compared with 51 associated with the rhizomes with the rhizomes dominated by the turf-forming red algal species *Acrothamnion preissii* and *Womersleyella setacea*, both introduced species. In a later study, Piazzi et al. (2002) looked at the rhizome assemblage in more detail and found that the functional diversity of the rhizome assemblage was low (mainly filamentous species) at sites where these introduced species were present and diverse when they were absent. The authors also attributed the absence of seasonal changes in the rhizome assemblages to the presence of these introduced species. They conclude that a competition between the introduced and native species plays an important role in structuring the rhizome algal assemblages and their spatial and temporal patterns. Peterson and Heck (2001) reported quite a different interaction. They introduced mussel mimics into a seagrass meadow and observed an increase in grazer density and decrease in epiphyte biomass. They suggest that the mussel shells provide shelter for epibenthic grazers, thereby creating greater grazing pressure on the epiphytes.

V. Conclusions

The seagrass epiphytes are an integral, complex, and dynamic component of seagrass ecosystems. They can make up a significant proportion of the total primary production of these ecosystems and are generally the primary food source for the associated fauna as well as contributing to detrital food webs. Epiphytes also provide shelter for many species. Normally, the seagrass epiphytes do not seem to have a detrimental effect on their seagrass host; however, under certain conditions that lead to a 'bloom' in the epiphytic algae they may contribute to the decline of the seagrass.

A lack of knowledge about the physiology of epiphytic algae also limits our ability to predict how they will respond to changes in nutrient availability and changes in the light environment. For example, and existing models of seagrass ecosystems need to make some major assumptions about the responses of epiphytic algae to changes in the environment (e.g. Plus et al., 2003). Furthermore, our understanding of the factors controlling seagrass epiphyte diversity and abundance is still limited by the nature of the complex interactions between physical factors (e.g. light, temperature, water movement, nutrients) and biological interactions (competition for space, grazing, and predation). Variability in the growth rate and longevity of the seagrass substratum further complicates experimental studies and data interpretation. The use of artificial seagrasses is one approach to reduce some of this variability and combined with well-designed natural and manipulative field experiments will lead to greater understanding of these communities.

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Chapter 20

The Central Role of Grazing in Seagrass Ecology

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"[F]or most of the past 50 My, Caribbean seagrass communities have had to withstand heavy, sustained grazing pressure from several sympatric lineages of large mammalian herbivores. This factor is almost totally absent both from these communities today (wherein manatees are scarce or absent in most areas) and from the thinking of the aquatic botanists and marine ecologists who study these communities. Consequently, the long-established tenet that seagrass ecosystems are largely detritus-based . . . must be revised to recognize that the modern situation is anomalous, and that the 'normal' pattern throughout most of tropical seagrass history has been that much (probably most) of the primary productivity has been channeled through the guts of herbivores, particularly sirenians." (Domning, 2001)

I. Introduction

Like kelps, salt marsh grasses, and mangroves, seagrasses are foundation species (*sensu* Dayton 1975) of important ecosystems. The physical habitat, production, and predation refuge they supply supports dense, diverse, and productive faunal assemblages (Kikuchi 1974; Klumpp et al. 1989; Valentine and Heck 1993; Williams and Heck 2001). Despite their dependence on seagrasses; however, animals living among the blades are hardly passive lawn ornaments. Both first principles and empirical evidence from other, better-studied systems strongly imply that seagrass fauna, dominated numerically by herbivores (Valentine and Heck 1999; Heck et al. 2000), should play central roles in mediating the structure and function of seagrass communities. In this chapter, we review evidence for such roles, attempt to place grazing—on both seagrass and attached algae—in the context of the larger food web and its influence on seagrass ecosystem structure and function, and discuss implications for management of seagrass-dominated ecosystems. As in all ecosystems, seagrasses and their associated communities are fundamentally influenced by the abiotic environment, including climate, light and nutrient regimes. There are several excellent recent reviews of abiotic influences on seagrass ecology (e.g. Hemminga and Duarte 2000), including chapters in this volume. Our focus on grazing is not meant to minimize the importance of these influences but to complement them, and to begin to address how abiotic drivers and consumers interact to shape seagrass ecosystem structure and function.

The relative importance of resource supply (bottom-up control) versus consumer influence (top-down control) in mediating the structure and functioning of communities and ecosystems is a fundamental issue in ecology, and has been hotly debated for decades. All ecosystems depend ultimately on primary producers, and thus, in an important sense, all ecosystems are ultimately regulated from the bottom-up (Hunter and Price 1992; Power 1992). Nevertheless, given a particular level of resource input, the habitat structure, community structure, biomass, and ecosystem process rates

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are profoundly influenced by consumers in many ecosystems (Hairston et al. 1960, Cyr and Pace 1993; Menge 1995; Duffy and Hay 2001; Shurin et al. 2002). Debate over the relative influence of bottom-up and top-down regulation in ecology began in earnest with the suggestion by Hairston et al. (1960) that, in terrestrial ecosystems, predator influence penetrates downward to regulate total plant biomass, in what has since become known (Paine 1980; Carpenter et al. 1985) as a trophic cascade. In essence, Hairston et al. (1960) suggested that top predators and alternating trophic levels below them are regulated by food availability, with intervening levels being regulated by predation. Thus in a system with three effective levels, abundances of predators and plants are controlled by resources (bottom-up) and herbivores by higher-order predators (top-down). That is, control of trophic level biomass should alternate between resource supply and consumer pressure at successive levels. A few empirical studies have dramatically confirmed such alternate control by resources and consumers at successive trophic levels (Wootton and Power 1993), and trophic cascades have been documented in a wide range of marine, freshwater, and terrestrial systems (reviewed by Brett and Goldman 1996; Micheli 1999; Schmitz et al. 2000; Halaj and Wise 2001; Shurin et al. 2002). Indeed, trophic cascades tend to be stronger, on average, in marine benthic systems than elsewhere (Fig. 1, Shurin et al. 2002). Nevertheless, a number of factors complicate the simple interactions among adjacent trophic levels predicted by the trophic cascade model, including functional diversity within levels, plant and prey defenses, omnivory, and intraguild predation, all of which dampen the ability of consumers to control accumulation of prey biomass at lower trophic levels (Murdoch 1966; Polis and Strong 1996; Polis 1999; Duffy 2002). Thus, the importance and generality of trophic cascades in nature, especially in diverse systems, remains controversial (e.g. Polis 1999; Persson 1999).

Herbivores are critical links between primary producers and higher trophic levels in all ecosystems. Herbivores strongly influence the biomass, productivity and community composition of plants in most aquatic and marine ecosystems (e.g. Porter 1973, 1977; Lynch and Shapiro 1981; Lewis 1985; Vanni 1987a; Cyr and Pace 1993; Mallin and Paerl 1994; Sterner and Elser 2002). In freshwater lakes, for example, zooplankton grazing can trigger dramatic shifts in the composition of phytoplankton assemblages away from smaller vulnerable species towards assemblages dominated by larger, gelatinous, or otherwise protected phytoplankton species (e.g. Porter 1973, 1977; McCauley and Briand 1979; DeMott and Kerfoot 1982; Vanni 1987b). Similarly, in benthic marine systems, intense grazing by fishes and invertebrates often shifts macroalgal dominance away from highly competitive, fast-growing, edible algae towards dominance by slowly-growing, defended seaweeds or sessile invertebrates that are less vulnerable to grazers (reviewed by Lubchencho and Gaines 1981; Gaines and Lubchencho 1982; Hay and Steinberg 1992; Steneck and Dethier 1994; Duffy and Hay 2001). Among the most spectacular examples of herbivore control is the conversion, by sea urchins, of three-dimensional kelp forests to depauperate, two-dimensional pavements of grazer-resistant coralline algae, with pervasive consequences for functioning of the nearshore marine ecosystem (reviewed by Lawrence 1975; Estes and Duggins 1995).

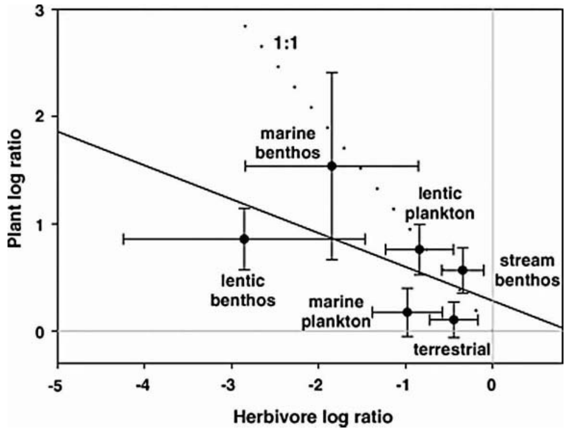

Fig. 1. Average effects of predators on herbivores, and on primary producers through trophic cascades, in six broad types of ecosystems, based on meta-analysis of experimental results (Shurin et al. 2002). Error bars are 95% confidence intervals. The effect of predators is significant if the confidence interval does not overlap zero (gray lines). The dotted line shows the 1:1 relationship, i.e. the relationship expected if predator effects cascade with no loss of efficiency directly to plants. Note that the strongest average effects of predators are found in marine benthic systems.

Whereas the central role of grazers in structuring macroalgal assemblages is well documented and widely recognized, we know less about the population- and community-level impacts of herbivores on seagrass ecosystems. Several factors probably contribute to this deficit. First, the complex physiology and demography of clonal seagrasses, and the presence of a substantial portion of their

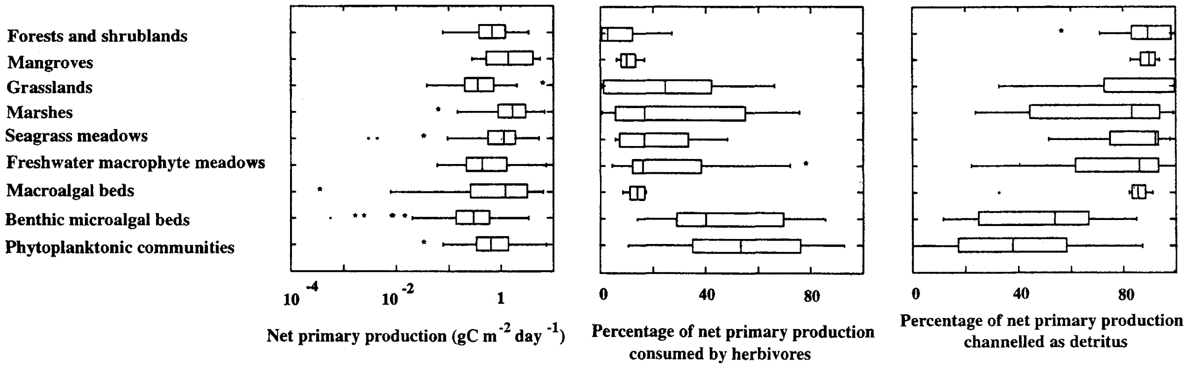

Fig. 2. Patterns in the fate of production in seagrass and other ecosystem types, based on a compilation of over 200 literature reports (Cebrián 1999). For each variable, boxes encompass the 25^{th} and 75^{th} quartiles of the data, and the central line represents the median. The proportion of seagrass production consumed directly by grazers varies up to about 50% but is low, on average, relative to algal-based aquatic ecosystems.

biomass within sediments, makes experimental manipulation of these plants difficult. Secondly, seagrass ecology has traditionally been dominated by classical investigations of plant physiology and the impacts of eutrophication on seagrass growth, with little attention to the community-oriented approaches employed effectively in other branches of marine ecology. Whatever the reason, we perceive (as have others, e.g. Williams and Heck 2001; Domning 2001) a lack of appreciation for the potentially critical role of grazing, historically and currently, in determining the structure and productivity of seagrass food webs. Indeed, one of the few existing paradigms of marine ecology is that little of the production of seagrasses is grazed by marine herbivores (e.g. Cebrián 1999, 2002; Mateo et al., Chapter 7; Fig. 2). In this chapter, we review existing information, and offer new hypotheses, for the current and historical role of grazing in the ecology and evolution of seagrasses, with particular reference to its role in mediating the relative dominance of seagrasses versus benthic algae. Our review leads us to suggest that the current bottom-up paradigm of seagrass ecology, which has focused primarily on control of seagrass populations by light, nutrients, and other abiotic variables, is incomplete. We review the substantial evidence that grazing—on either living seagrasses, or their attached epiphytic algae—is of critical importance in mediating population dynamics, community composition, and materials fluxes in seagrass ecosystems. A unifying theme that emerges from our analysis is that trophic interactions generally, and grazing in particular, can have pervasive impacts on many aspects of the population, community, and ecosystem ecology of seagrass beds. Moreover, seagrass morphologies, growth patterns, and life histories are likely to have been molded by historical grazing regimes quite different than those prevailing today. In short, we propose that the structure and functioning of seagrass ecosystems cannot be understood except in the context of the larger food webs they support. Although we find the weight of evidence for these points compelling, there is a clear need for more and better experimental research focused on the role of trophic interactions in the ecology of seagrass systems. Accordingly, we close our chapter by suggesting several hypotheses that we hope will stimulate new approaches to assessing the organization and dynamics of seagrass ecosystems, and their importance in supplying production to marine food webs.

II. Philosophy of the Review

The basic qualitative biology of herbivory in seagrass beds is reasonably well known. Despite considerable variance in feeding strategies among species, we can generalize that vertebrate herbivores (fishes, turtles, sirenians, and waterfowl) and sea urchins often graze seagrasses directly, whereas smaller mesograzers (crustaceans, gastropods, and other invertebrates) usually feed on algae attached to seagrass leaves. These patterns have been thoroughly documented by previous reviews (Orth and van Montfrans 1984; van Montfrans et al. 1984; Thayer et al. 1984; Klumpp et al. 1989; Jernakoff et al. 1996; Valentine and Heck 1999; Williams and Heck 2001).

Given the strength of these previously documented generalizations, which we update below, we focus here on placing grazing in the larger context of seagrass community and ecosystem dynamics. The time appears ripe to ask new questions such as the following: What environmental and biological factors influence grazing intensity? How frequently and strongly do grazers control seagrass biomass and density? How does grazing influence seagrass beds at the community level, particularly the relative dominance of seagrasses, macroalgae, microalgae, and sessile invertebrates? How does grazing influence ecosystem process rates (e.g. primary productivity, metabolism, and materials fluxes) in seagrass beds? Moving up a trophic level, how is grazing impact influenced by cascading predator control, and to what extent has this control been altered by the overfishing of larger marine piscivores? In short, what would seagrass beds look like and how would they work in the absence of grazers? Indeed, would they even exist in the absence of grazers? Although most of these questions cannot be answered at present, we hope this review will stimulate research focused on doing so.

III. An Evolutionary Perspective on Seagrasses and their Grazers

To put the role of grazing in seagrass systems in perspective, we begin with a long-term evolutionary perspective, inspired by comparisons with terrestrial grasses and the steppe-dominated ecosystems whose food webs are dominated by large herds of grazing ungulates. It is generally appreciated that the plants of these terrestrial grassland ecosystems share a long and close evolutionary history with large vertebrate grazers, and that important traits of both the grazers and the grasses represent, at least in part, adaptations to their long and intense coevolutionary interactions (Barnard and Frankel 1964; Mack and Thompson 1982; McNaughton 1984; Coughenour 1985). Many of these ungulates are characterized by dental adaptations resulting from grazing on gritty, silica-rich grasses. Terrestrial grasses, in turn, developed belowground basal meristems, rhizomes, adventitious fibrous roots, clonal propagation through tillering, rapid growth of deciduous leaves, high tolerance to partial defoliation, and other traits that minimize the impacts of sustained grazing by herds of these large grazers. Grasses with these traits dominate most heavily grazed terrestrial ecosystems, although they are also present in many ungrazed areas. Similarly, wherever large domestic grazing livestock have been introduced, rhizomatous grasses with the same suite of traits, whether native or alien, are dominant. These trends, along with the simultaneous rise of extensive grasslands and diverse grazing ungulates, support the premise that rhizomatous grasses have coevolved with chronic grazing by large vertebrates, even if some originally arose as adaptations to drought tolerance (Barnard and Frankel 1964; Coughenour 1985).

Seagrasses evolved independently of terrestrial grasses (Larkum and Den Hartog 1989; Les et al. 1997), but these two groups are convergent in several conspicuous respects. Interestingly, seagrasses share many of the same features with terrestrial grasses discussed above, which have been suggested as adaptations to heavy grazing pressure. These include clonal propagation and resultant physiological integration of ramets, in many cases the possession of largely inaccessible belowground basal meristems and branching rhizomes, an abundance of small deciduous shoots, and often rapid regeneration of defoliated tissues (Valentine and Heck 1999; Valentine et al. 2004). There are, of course, many possible adaptive benefits of such growth patterns. Nevertheless, the convergent presence of these morphological, growth, and life history characters in many seagrasses, which are widely understood to represent adaptations to chronic grazing in terrestrial grasses, suggests the intriguing possibility that seagrasses also may have evolved under an historical regime of intense and regular grazing. Who might have been responsible for such grazing? In modern ecosystems, certain fishes, sea turtles, sea urchins and waterfowl feed directly on seagrasses and can have important impacts on them, as we document below. But the grazers that have had the strongest ecological and evolutionary impacts on seagrasses over time have probably been the green turtles, sirenians including dugongs and manatees, and waterfowl (Valentine and Heck 1999; Domning 2001). Extant sirenians and some waterfowl feed preferentially or even obligately on seagrasses, and include the only animals known to feed on seagrass rhizomes. Sirenians were both diverse and abundant in warm marine waters prior to the Pleistocene, and appear to have been closely associated with seagrasses throughout their 50 My history. Many dugongine sirenians evolved large blade-like tusks that were probably adaptations to uprooting and feeding on the large, tough rhizomes of seagrass taxa such as *Thalassia* and *Zostera*. Indeed, after reviewing the fossil history of both seagrasses and sirenians in the Caribbean region, Domning (2001) concluded that "for most of the past 50 Ma, Caribbean seagrass communities have had to withstand sustained grazing pressure from several sympatric lineages of large mammalian herbivores" (p. 45); "Under these conditions (which prevailed up to about 2-3 Ma), most primary productivity was presumably consumed by herbivores, in contrast to the detritus-based seagrass ecosystems of today, which include few if any large herbivores" (p. 27). These conclusions may even understate the historical dominance of seagrass grazing given the formerly great abundances of seagrass-grazing green turtles and perhaps waterfowl (Jackson et al. 2001). Thus, in past times grazing vertebrates in seagrass beds may have been as important in determining productivity as they were in terrestrial grasslands (cf. McNaughton 1984).

IV. The Modern Seagrass Community Interaction Web

Today the situation is quite different. For the most part, large vertebrate grazers of seagrasses are functionally extinct, due to human exploitation, throughout most of the global ocean (Jackson et al. 2001). Thus, many modern seagrass ecosystems are of the detritus-based type, with little seagrass production grazed directly (Fig. 2, Cebrián and Duarte 2001; Cebrián 1999, 2002; Mateo et al., Chapter 7). Although waterfowl and sparid fishes have locally intense impacts on seagrass biomass in some areas, the most abundant primary consumers in most temperate seagrass ecosystems are smaller invertebrate mesograzers that feed mainly on algae attached to seagrass leaves (Kikuchi 1974; Orth and van Montfrans 1984; Klumpp et al. 1989; Jernakoff et al. 1996). In many warmer seas, seagrasses are intensely grazed by sea urchins and some fishes (Thayer et al. 1984; Valentine and Heck 1999). Thus, the major components in a generalized seagrass food web must include at least the following: seagrasses and their attached algae, invertebrate mesograzers, detritivores, vertebrate grazers, small invertebrate-feeding predators, piscivorous predators—and, of course, humans (Fig. 3). Direct and indirect interactions among these functional groups have potentially important influences on the relative dominance of seagrasses, macroalgae, and microalgae, as shown by growing experimental evidence from seagrass beds (see below), and inferences drawn from other ecosystems. Understanding the functioning of seagrass ecosystems, and predicting and mitigating their responses to anthropogenic stresses, requires understanding these food-web processes and how they interact with changing resource fluxes.

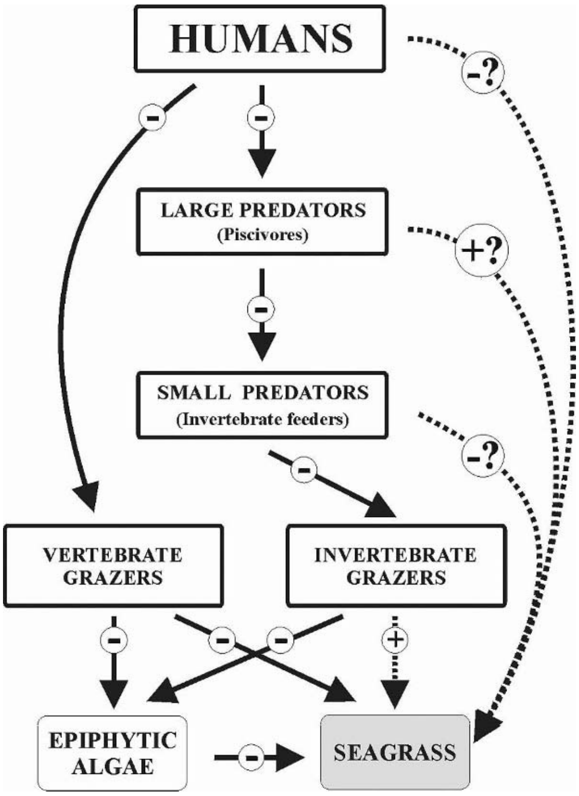

Fig. 3. Schematic illustration of a simplified seagrass-bed food web. Solid and broken arrows indicate direct and indirect effects, respectively. Plus and minus signs indicate positive and negative effects, respectively, that one class of organisms has on another, in the direction of the arrow. Indirect, cascading effects of humans and other predators on seagrasses are indicated with question marks, reflecting the current inadequacy of data to evaluate these potential effects. Note that the hypothesized human impacts include only those mediated through the food web, not those resulting from eutrophication and other disturbances (see Fig. 6).

Herbivores occupy a central role in determining the structure and productivity of most marine food webs. Not only can grazers influence the biomass, productivity, and community structure of primary producers (Lubchenco and Gaines 1981; Cyr and Pace 1993; Menge 1995; Shurin et al. 2002), they are also an important conduit for the transfer of energy from primary producers to higher trophic levels. Thus, grazers exert an important bottom-up control over the nutritional status, abundance, and composition of higher-order consumers. This is especially true of the small invertebrate mesograzers, the key link between primary producers and higher trophic levels in shallow marine systems (Edgar and Shaw 1995; Taylor 1998). As such, the influence of grazers cascades both downwards and upwards in food webs. Accordingly, the roles of grazers can be approached from two distinct perspectives, focusing on their influence on community structure, versus on ecosystem processes. Paine (1980) emphasized that these two types of influence, which he referred to as functional webs (also called interaction webs) versus energy-flow webs, respectively, are often not necessarily concordant. That is, a trophic link with negligible influence on energy and materials flows under normal circumstances, can nonetheless have a critical influence on the relative abundance of species in the community (Paine 1980), and on the system's stability (McCann et al. 1998; Berlow 1999). Similarly, key conduits for the transfer of energy among adjacent trophic levels need not be strong interactors from a community perspective (e.g. Kirsch et al. 2002).

Below we consider both the community-level and ecosystem-level influences of grazing. We consider separately the mostly tropical systems in which direct grazing of seagrasses can still be substantial, and the invertebrate-dominated, mostly temperate systems in which grazers feed primarily on attached epiphytic algae, and impacts on seagrasses are primarily indirect.

V. Direct Grazing on Seagrasses

A. Is Direct Grazing on Seagrasses Negligible?

One of the few existing paradigms of marine ecology holds that, in most systems, little seagrass primary production is directly grazed (Fig. 2). Most marine texts report that, on average, <30% of seagrass production reaches higher order consumers via the grazing pathway (e.g. Lalli and Parson 1993; Valiela 1995; Levinton 2000; Nybakken 2000; see also Mateo et al., Chapter 7). As a result, the primary conduit for seagrass production to reach higher order consumers is consistently reported to be the detrital pathway (e.g. Fenchel 1970, 1977; Kikuchi and Peres 1977; Nienhaus and Van Ierland 1978; Kikuchi 1980; Thayer et al. 1984; Nienhaus and Groenendijk 1986; Zieman and Zieman 1989; Cebrián 2002; Mateo et al., Chapter 7). One contributory factor to this view is the observation that in seagrass systems, as in most systems on land, "the world is green" (Hairston et al. 1960). That is, since seagrasses form lush vegetated habitats along the coasts of every continent except Antarctica, herbivores would seem unlikely to play a significant role in controlling their biomass. Despite this plausible qualitative picture, there have been relatively few critical assessments of the importance of grazing in seagrass beds, and fewer direct estimates of the proportion of seagrass production consumed in the field. Consequently, investigations of the factors controlling seagrass growth and biomass emphasize the primacy of the sediment nutrient supply (e.g. Patriquin 1972; Short 1987; Powell et al. 1989; Fourqurean et al. 1992; Short et al. 1993), light availability, and/or physical factors (e.g. Patriquin 1975; Backman and Barilotti 1976; Dennison and Alberte 1985; Thom and Albright 1990).

The history of this "bottom-up" paradigm for seagrass ecosystems is intriguingly similar to the analogous worldview of early terrestrial ecologists, who also perceived grazing on terrestrial plants to be low. Just as early assessments of terrestrial plant-animal interactions are now known to have been overly simplistic (e.g. Karban and Baldwin 1997; Lowman 1984, 1985; McNaughton 1985; McNaughton et al. 1996), it is increasingly clear that seagrass-grazer interactions are more important and dynamic than previously recognized. In this section we provide an updated overview of recent evidence of direct grazing on seagrasses. Perhaps surprisingly, there is ample evidence that grazing on seagrasses is significant in many areas of the world's oceans. This evidence suggests that it is premature to conclude in general terms how important direct grazing of seagrasses is in determining the structure and productivity of modern coastal food webs.

Two distinct, but not mutually exclusive, explanations have been offered for the apparently low levels of herbivory on seagrasses. These can be classified roughly as bottom-up and top-down hypotheses. The first suggests that seagrass physiology results in low nutritional value that poses an intrinsic barrier to grazers. Specifically, the suggestion has been made that seagrass leaves are of little nutritional value owing to their high C/N ratios (e.g. Bjorndal 1980; Duarte 1990; Mateo et al., Chapter 7), and the inability of most grazers to digest cellulose (Lawrence 1975). The second hypothesis recognizes that several herbivores are capable of grazing and assimilating seagrass tissues, but posits that human overharvesting and other activities have left densities of these ecologically important large vertebrate seagrass grazers (the green turtles, dugongs, manatees, fishes, and waterfowl) anomalously low (Randall 1965; Heinsohn and Birch 1972; Lipkin 1975; Charman 1979; Bjorndal 1980; Kiorboe 1980; Jacobs et al. 1981; Thayer et al. 1984). These hypotheses are not mutually exclusive, as poor nutritional quality could deter many generalist herbivores, whereas human hunting may have reduced the densities of those specialists capable of grazing seagrasses. We consider each of these hypotheses in turn.

B. Nutritional Value of Seagrasses

Several investigators have shown that, in contrast to the poor-nutrition hypothesis, nitrogen concentrations of seagrass leaves are not dramatically lower, when compared on a standardized basis, than those of algae that form the base of most marine food webs (Lobel and Ogden 1981; Lowe and Lawrence 1976; Thayer et al. 1984; Strong 1992; Pillans et al. 2004; see also Section III.A in Mateo et al., Chapter 7 and their Fig. 4). There is also evidence that detrital seagrass leaves can be an even poorer source of nutrition (i.e. have higher C/N ratios) for consumers than are living leaves (Klumpp and Van der Walk 1984), as seagrass detritus resists decay (Zieman 1975; Harrison and Mann 1975; Fenchel 1977; Thayer et al. 1977; Rice 1982). The use of C/N ratios as criteria to assess the nutritional value of marine macrophytes can be traced to Russell-Hunter (1970) who concluded that food with a C/N ratio <17 was required to satisfy human protein requirements. While the C/N ratio has been correlated with growth of some pelagic freshwater herbivores (Elser et al. 2003), it has not been clearly linked to performance of marine herbivores (cf. Thayer et al. 1977; Hatcher 1994). Therefore, it seems unlikely that high C/N ratios (>17), by themselves, are responsible for the relatively low grazing on seagrasses.

Many marine herbivores, in fact, have morphological adaptations or digestive capabilities that allow them to obtain nutrients and energy from marine vascular plants. Some fishes have low gut pH, allowing them to digest cellulose (e.g. Lobel 1981; Lobel and Ogden 1981; Montgomery and Targett 1992), while other fishes, reptiles, and sirenians (i.e. manatees and dugongs) possess microbial symbionts capable of digesting cellulose in seagrass leaf tissues (Bjorndal 1979; Thayer et al. 1984; Luczkovich and Stellwag 1993). In addition, the presence of calcareous epiphytes on surfaces of some seagrass leaves may play an important role, in enhancing assimilation of seagrass tissue in some fishes (T. Arnold, per. comm.). These observations have led some to conclude that, as has been suggested for many herbivorous insects and mammals, herbivore feeding on seagrasses is determined largely by nitrogen availability, rather than by carbon content (e.g. Boyd and Goodyear 1971; Mann 1972; Lilly 1975; Bjorndal 1980; Zieman et al. 1984; Williams 1988; McGlathery 1995; Preen 1995, this chapter). Thus, it is unclear whether low nutritional value of seagrass tissues is a major impediment to grazing, at least by vertebrates.

C. The Ghost of Grazing Past

Mounting evidence indicates that human fishing and other activities have had strong, far-reaching, and sometimes catastrophic impacts on large marine animals throughout the world (Jackson et al. 2001; Pauly and Maclean 2003; Myers and Worm 2003). The ecosystem-level impacts of these declines in consumer density can only be estimated indirectly, but they are surely large (Jackson et al. 2001; Duffy 2003). In particular, severe reductions in abundance of large vertebrate grazers (notably green turtles and sirenians but also waterfowl) have almost certainly reduced the importance of herbivory in seagrass food webs (Madsen 1998; Domning 2001). Despite these upheavals, some marine food webs have sufficient functional redundancy that the remaining herbivores continue to have significant effects on aboveground seagrass biomass (next section, Table 1), even if it is neither as intense, nor as consistent in space and time, as it once was. The suggested impacts of these historical reductions in grazing pressure are difficult to evaluate; however, because there have been few controlled field experiments designed to determine the degree to which modern herbivores impact

Table 1. Summary of selected studies or reports of herbivory in seagrasses. (W) = waterfowl; (U) = urchin; (G) = gastropod; (C) = crustacean; (F) = fish; (R) = reptile (M) = mammal. This table is updated from Valentine and Heck 1999.

Grazer	Seagrass, location, study type	Description of results	References
Aythya americana (W)	*Halodule wrightii*. Lower Laguna Madre, TX. Two years of field collections and one experiment at 3 sites were used to assess impacts of redhead ducks on SAV biomass.	Rhizome biomass was 75% lower in grazed areas than where grazers were excluded. When rhizome biomass was grazed below 0.18 gms/DM/core (at 1/3 of the sites) grass did not recover.	Mitchell et al. 1994
Aythya americana (W)	*Halodule wrightii*, Chandeleur Sound, Louisiana. Field monitoring of seagrass biomass to document the impact of waterfowl grazing on seagrass.	Waterfowl grazing was found to reduce aboveground and belowground biomass by 90 and 49%, respectively.	Michot and Chadwick 1994
Anas crecca (W), *Anas penelope* (W), *Branta bernicla bernicla* (W),	*Zostera noltii* and *Z. marina.* Solent, England. Field study, percent cover recorded at 5 stations. Exclosures used to monitor seagrass change due to grazing.	Large reductions in seagrass areal coverage attributed to Brent geese feeding.	Tubbs and Tubbs 1983
A. penelope (W), *A. platyrhyncha* (W), *A. acuta* (W), *B. bernicla* (W),	*Z. noltii* and *Z. marina*. Dutch Wadden Sea. Field-based bioenergetic study and field experiment where changes in SAV shoot density, biomass, and percent cover were monitored.	An estimated 1426 kg DW of seagrass (∼50% of all SAV production) consumed, mostly by *A. acuta* and *A. penelope*.	Jacobs et al. 1981
A. acuta (W), *Anas americana* (W), *A. platyrhynchos* (W), *Branta bernicla* (W)	*Zostera japonica* and *Z. marina*. Boundary Bay, British Columbia. Collections and field based bioenergetic study. Above- and below ground standing stock were monitored. Waterfowl use days were estimated. Some birds were collected and esophagus contents recorded.	Bird density positively correlated with SAV distribution. Dabbling ducks and geese consumed some 362 t of *Z. japonica* leaves and rhizomes (∼50% of aboveground and 43% of belowground biomass) at the study site. Lesser amounts of *Z. marina* consumed.	Baldwin and Lovvorn 1994
Anas crecca (W), *Anas penelope* (W), *Branta bernicla* (W)	*Zostera noltii* and Zostera *marina*. Dutch Wadden Sea. Field surveys plus an exclosure experiment were used to quantify impacts of wildfowl grazing on seagrass biomass.	Brent geese and widgeon reduced aboveground biomass some 30% faster than in areas where grazers were excluded. Belowground biomass in grazed cages was 48% lower than in ungrazed plots.	Madsen 1988
A. acuta (W), *A. creeca* (W), *Aythya ferina* (W), *Anas penelope* (W), *A. platyrhynchos* (W), *Branta bernicla* (W), *Cygnus olor* (W), *Fulica atra* (W), *Idotea chelipes (C)*	*Zostera marina*. Lake Grevelingen, SW Netherlands. Field based bioenergetic study and laboratory experiment.	An estimated 7.5% of *Zostera* marina production consumed by waterfowl and a single species of isopod.	Nienhuis and Groenendijk 1986
Anas penelope (W). *Branta bernicla hrota* (W),	*Zostera* sp., Strangford Slough., northern Ireland. Field study. The impact of grazers was documented by monitoring changes in seagrass biomass at the study area along with the use of exclusion cages in grassbeds with uniform coverage.	Grazing led to faster rates of seagrass loss than was occurring due to weathering in ungrazed areas. Belowground biomass was 48% lower in grazed plots than measured in ungrazed plots.	Portig et al. 1994

Lytechinus variegatus (U)	*Thalassia testudinum*. Offshore grass beds of west Florida. Field observations and measurements.	An episodic settlement of sea urchins led to significant reductions of seagrass coverage of some. Grazing was found to denude an estimated 20 hectare area of seagrass habitat.	Camp et al. 1973
L. variegatus (U) and *Tripneustes ventricosus* (U)	*Thalassia testudinum*. Discovery Bay, Jamaica. Field experiment tested for intra- and interspecific competition between two species of urchins. Aboveground biomass within cages was used to document the effects urchin manipulations.	*Tripneustes* grazing had a highly significant effect on seagrass biomass in enclosure treatments. *Lytechinus* had a moderate effect on seagrass biomass.	Keller 1983
L. variegatus (U)	*Thalassia testudinum*. Biscayne Bay Florida. Laboratory estimate of sea urchin ingestion rates and preferences when fed live seagrass and seagrass detritus.	Urchins ingested decayed leaves at a significantly higher rate than when fed green leaves. No evidence of a significant preference for decayed leaves over green ones was found.	Montague et al. 1991
L. variegatus (U)	*Thalassia testudinum*. Miskito Cays, Nicaragua. Laboratory measurements, field collections and observations. Feeding preferences determined by turning over urchins. Urchin gut contents examined at one station.	Sea urchins were estimated to consume some 0.5 g DW/urchin/day of seagrass. However, gut contents indicated that 40% of this urchin's diet was detrital turtlegrass. Less than 5% of the diet was live grasses.	Vadas et al. 1982
Mixed grazer assemblage including: L. variegatus (U), *Sparisoma radians* (F) *Archosargus rhomboides* (F), *Monocanthus setiferus* (F), *Acanthurus chirurigus* (F), *Sphaeroides spengleri* (F), and *Acanthostracion quadricornis* (F)	*Thalassia testudinum*, Kingston Harbour Jamaica. Laboratory measurements, field sampling, stomach content analysis, and field experimentation to estimate herbivory on grazers on seagrass.	5 species of fish found to feed on both live and detrital seagrass along with algae and crustaceans. Only the sea urchin *Lytechinus* and the buck tooth parrotfish *S. radians* were found to feed predominantly on seagrass. *Lytechinus* was estimated to consume some 49% of the SAV leaf tissue produced each day. A small fraction of this production was consumed by fishes.	Greenway 1976 and 1995
L. variegatus (U)	*Thalassia testudinum*. Card Sound Florida. Field Observations.	A large population of sea urchins consumed all benthic plants in a several hectare area of Card Sound.	Bach 1979
Tripneustes gratilla (U)	*Thalassodendron ciliatum.* Mombassa lagoon, Kenya. Multiple sampling approaches and mathematical estimates were used to determine the degree to which sea urchins impact seagrass density and coverage.	Urchins grazing was found to exert a controlling influence over T. ciliatum density in Mombassa Lagoon.	Alcoverro and Mariani 2002
Tripneustes gratilla (U), Salmacis sphaeroides (U)	*Thalassia hemprichii*. Bolinao, Phillippines. Field and laboratory measurements of sea urchin consumption of seagrass biomass. Food preferences for several plant species also examined.	Preferences tests showed *Tripneustes* chose live SAV alternative food choices. *Salmacis* consumed equal quantities of all plant species. Both urchins efficiently digested and absorbed seagrass (>60%). Estimates of total SAV consumption by both sea urchins was 240–400 g DW/m^2/day, an average of ~17% of SAV produced with a range from 3–100% of SAV production).	Klumpp et al. 1993

(cont.)

Table 1. (Cont.)

Grazer	Seagrass, location, study type	Description of results	References
Paracentrotus lividus (U)	*Posidonia oceanica*. Mediterranean Sea. Field experimentation used to determine grazing impacts on seagrass biomass, shoot density, and production.	Loss of seagrass biomass was directly proportional to grazing intensity.	Kirkman and Young 1981
Paracentrotus lividus (U), *Sarpa salpa* (F)	*Posidonia oceanica*. Southeastern Spain, Mediterranean Sea. Field surveys, measurements of plant growth and ambient nutrients prior to and after the onset of aquaculture of a seagrass habitat. Estimates of grazing intensity were made based on the frequency of leaf tips damaged by urchins or fish.	Seagrass coverage diminished greatly after the commencement of aquaculture activities. Herbivore grazing was found to be intense near the aquaculture facility and it was hypothesized that this increased grazing played a significant role in the reduction of seagrass coverage. This elevated level of grazing was attributed to aquaculture induced improvements in the palatability of Posidonia leaves for local herbivores.	Ruiz et al. 2001
Astropyga magnifica (U)	*Zostera marina*. Tomioka Bay, Amakusa, Japan. Eelgrass patch size, density and biomass used to document the impact of a sea urchin aggregation on seagrass density. Urchin gut contents were recorded as well.	A seagrass patch was reduced form $\sim$71 to $<$3 m^2 in three months by grazing. Urchin stomachs were completely full of seagrass. No other plants were observed. The seagrass standing crop decreased from 7789 g DW to 375 g DW.	Bak and Nojima 1980
Heliocidaris erythrogramma (U)	*Posidonia australis*. Botany Bay, Australia. Field observations and mapping from 1930 1985 were used to document the impact of urchin grazing on a seagrass meadow.	Urchins completely denuded 20 ha of seagrass from 1979–1982 before being dispersed by a storm. Urchin aggregations reappeared in late 82 and an additional 25 ha of *Posidonia* was lost from 82–84. Up to 1987 no regrowth had occurred.	Larkum and West 1990
Tripneustes gratilla (U)	*Halophila stipulacea*. Sinai, Northern Red Sea and the Jordanian coast of the Gulf of Aqaba. Field observation.	Heavy urchin grazing was recorded on seagrasses at depths ranging from 5 m to 9 m. Grazing on seagrass was subsequently verified by gut content analysis.	Lipkin 1979; Bouchon 1980; Hulings and Kirkman 1982; Jafari and Mahasneh 1984
Temnopleuris michaelsenii (U)	Cockburn Sound, Warnbro Sound, Australia. Field sampling and seagrass mapping were used to document urchin denudation of a seagrass habitat.	In Cockburn Sound, seagrasses were grazed by locally abundant *Temnopleuris michaelsenii*. Most heavy damage was localized. Where grazing was heavy, plants had not recovered 2–4 years later. Urchins invaded a second site, reducing remnants of a one healthy seagrass meadow to bare sand. Intense grazing was noted in fall of three different years. Outbreaks were also reported from a third site, where sea urchins removed all of the leaves in deeper portions of a seagrass bed.	Cambridge et al. 1986

Tectura depicta (G)	*Zostera marina*. Monterey Bay, CA. Lab Experiment. *Zostera* transplanted into plastic flower pots, at natural densities of limpets were maintained on eight plants while 8 others kept grazer free. Seagrass growth was determined weekly along with total leaf length. At the tend of the experiment, plants were harvested and analyzed for biomass (shoot, rhizome, root), rates of leaf photosynthesis, respiration, and sucrose enzymes were measured in leaves and shoots, plus protein and sugar contents. Chlorophyll *a* was extracted from leaf segments.	Growth rates, carbon reserves, root proliferation, and net photosynthesis of grazed plants were 50–80% lower than on ungrazed plants. The carbon allocated to the roots of ungrazed plants was 800% higher for ungrazed plants than for grazed plants. Limpet grazing induced carbon limitation in eelgrass growing in an otherwise light replete environment.	Zimmerman et al. 1996
Littorina sitkana (G), *Margarites helicinus* (G), *Lacuna variegata* (G), *Telmessus chieragonus* (C), *Microcottus sellaris* (F), *Branta canadensis* (W), *Anas carolinensis* (W), *Anas acuta* (W)	*Zostera marina.* Izembek Lagoon, Alaska. Sampling and 13C:12C analysis.	Eelgrass was found to be incorporated into the local food chain through herbivory by at least 7 species.	McConnaughey and McRoy 1979
Ampithoe spp. (C)	*Syringodium isoetifolium* Fiji. Laboratory determinations of ingestion rates of manatee grass.	Initially amphipods fed at the top of the leaf. One day later they made nests from fragments of grazed grass. Grazing rates ranged from 1.7 mg ww/ind/day to 26.4 mg ww/ind/day. Using a carbon budget approach the authors estimated that the amphipods grazed of the material produced and further assimilated of it.	Mukai and Iijima 1995
Monocanthus chinensis (F)	*Posidonia oceanica*. Quibray Bay, Botany Bay, New South Wales. Stomach analysis and field sampling. ^{14}C labeled seagrass used to assess seagrass assimilation by fishes.	Gut analysis showed fish ate SAV, along with 5 spp of algae, crustaceans, and other invertebrates. Seagrass and amphipods were most abundant in fish guts. Microscopic examination of ingested plant material suggested that plants were untouched. (i.e., no cell wall damage observed). However, radioactive labeling showed that ~22% of labeled SAV was in the liver and gut wall of the fish, 32–33% in the feces. The remaining label may have been in other tissues. This is significant as it shows that microscopic examination of the cell walls does not necessarily provide a complete picture. The actual % of SAV production removed was low.	Conacher et al. 1979
Nectocarcinus inegrifons, (C), *Hyporhamphus melanochir* (F)	*Posidonia oceanica*. Victoria Australia. Gut content and biochemical marker analyses were used to the importance of seagrass production to the local food web.	Lipid and sterol analyses found that both *Nectocarcinus inegrifons*, and *Hyporhamphus melanichir* were found to rely heavily on seagrass production to meet their nutritional needs.	Nichols et al. 1986

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Table 1. (Cont.)

Grazer	Seagrass, location, study type	Description of results	References
Monacanthus chinensis (F), *Meuschenia freycineti* (F), *Meuschenia trachylepis* (F)	*Posidonia australis*. Port Hacking, N.S.W. Field sampling and stomach contents. The entire fish community in a 400 m^2 area of *Posidonia* was collected on twice each in 2 seasons. Stomachs of all leatherjackets were dissected and the contents identified. The relative percentages of food items were determined. Rectal items were identified using microscope to determine which items were used as food.	Leatherjackets dominated the fish community, averaging 26% of the number and 34% of the biomass. Seagrasses ingested were small pieces leaf material which was covered with epibionts. *M. freycineti* consistently bit off pieces in neat semicircular bites. Juveniles of all species of fed principally on encrusting animals listed above with little seagrass being present. Microscopic rectal contents from several inds. of each species found that *Posidonia* was undigested.	Bell et al. 1978
Monacanthus ciliatus (F) and *Stephanolepis hispidus* (F)	*Thalassia testudinum*. Apalachee Bay, FL. Field sampling and stomach contents of Filefish collected over a nine year period.	These fish fed on a wide variety of prey; however, five groups of seagrass, and invertebrates accounted for 80% of the stomach contents. As fish grew, the dietary importance of seagrasses and associated epifauna increased. Approximately of the diet of larger fishes was *Thalassia*. The pattern was the same for both species of filefishes. The incidence of SAV in the diets of *Monocanthus* was greatest in late summer and early fall coincident with peak SAV productivity. The incidence of SAV in *Stephanilepas* increased between summer and fall.	Clements and Livingston 1983
Hyporhamphus unifasciatus (F)	*Ruppia maritima* and *Halodule wrightii*. Crystal River, FL. Shallow water fish collected with a bag in approximately 1m of water.	Volume of SAV in gut ∼50% in large halfbeaks.	Carr and Adams 1973
Hyporhamphus melanochir (F)	*Zostera muelleri* and *Heterozostera tasmanica* Cirb Point, Western Port Bay, and Duck Point, Corner Inlet, Australis. Field sampling and stomach contents.	During the day green eelgrass tissue was in the guts of 93% of the fish, making up almost 70% of the total volume. Insects, amphipods, and shrimp larvae made up most of the remaining food. Amphipods were far more important prey at night. Eelgrass tissue was consumed by 1/3 of fish and was only 18% of total volume at night. All eelgrass material in the guts was macerated by pharyngeal teeth. Eelgrass in the foregut was undigested, while material in the hindgut was colorless. Microscopic examination of the material found most plant cells were empty.	Robertson and Klumpp 1983
Arrhamphus sclerolepis krefftii (F)	No specific species of seagrass listed. South east Queensland, Australia. Histological examinations of *A. sclerolepis krefftii* were conducted to determine how garfish can assimilate nutrients from ingested seagrass leaves.	This study found than mucousal cells in the alimentary canal of this garfish could assimilate seagrass production.	Tibbetts 1997

Lagodon rhomboides (F)	*Zostera marina*. Field sampling and Laboratory Bioenergetic and radioactive labeling study. Pinfish (>65 mm SL) were fed diets of either eelgrass or frozen grass shrimp. Assimilation efficiency for plants (either eelgrass or algae) and shrimp and labeled seagrass.	Pinfish found to assimilate a substantial portion of the organic material from eelgrass, but with less efficiency than shrimp. Specific growth rates of pinfish fed grass shrimp partially substituted with either eelgrass or digestible carbohydrates were not significantly different from growth rates when feeding solely on shrimp. Pinfish appeared to increase feeding rates when offered low calorie seagrass.	Montgomery and Targett 1992
Sparisoma rubripinne (F) *and Sparisoma chrysopterum* (F)	*Thalassia testudinum*. Carrie Bow Cay, Belize. Field tethering study using clean freshly collected pieces of *Thalassia* blades along with algal species.	Each study found that herbivorous fishes readily consumed seagrass leaves but the intensity varied according to coral reef habitat and depth. Lewis found that tethered *Thalassia* was entirely consumed by two parrotfish- *Sparisoma rubripinne* and *Sparisoma chrysopterum*. Lewis also found that *Thalassia* was among the preferred sources of food during feeding trials.	Hay 1981; Lewis 1985
Sparisoma radians (F)	*Thalssia testudinum*. Northern Florida Keys. Field tethering. Study that compared tissues losses to bucktooth parrotfish with net aboveground turtlegrass production at multiple site.	This study found that grazing intensity varied greatly both spatially and temporally. Some 80% if annual net aboveground turtlegrass production was consumed.	Kirsch et al. 2002
Scarus spp. (F), *Sparisoma* spp (F), *Acanthurus* spp. (F)	*Thalassia testudinum*, *Halodule wrightii*. US Virgin Islands. Field experiment, stomach contents and observation. Three separate transplantation of mixed plots *Thalassia* and *Halodule* were into a halo zone next to a coral reef used to assess the impact of herbivores on seagrass abundance. In addition, an artificial reef was built at in a mixed Turtlegrass and *Halodule* habitat.	Parrotfish totally consumed seagrass patches transplanted into a halo zone next to a coral reef. Parrotfish (*Scarus* and *Sparisoma*) all seem to feed to some degree on the grass, *Scarus guacamaia* had 95% of the gut volume filled with *Halodule*. *Acanthurus chiurugis* and *A. bahamensis* had 40 and 80% gut volume filled with seagrass.	Randall 1965
Scarus guacamia (F) *and Sparisoma radians* (F)	*Thalassia testudinum*. St; Croix, USVI. Sampling. Seagrass leaves collected and fish bites marks identified along a transect running from the base of a coral reef into an adjacent seagrass habitat.	Leaves collected closest to a reef showed bites resulting from a population of large parrotfishes (*Scarus guacamia*) whereas the stations 20 and 60 m from the reef had bites characteristic of *Sparisoma radians*. The station 4 m from the reef showed mixed feeding.	Ogden and Zieman 1977
Scarus croicensis (F), Sparisoma aurofrenatum (F), Acanthurus chiurugus (F), A. bahianus (F)	*Syringodium filiforme and Thalassia testudinum*. San Blas Islands, Panama. Field tethering study measured both feeding selectivity and intensity.	Each species of seagrass was heavily grazed but herbivory on these grasses was variable spatially.	Tribble 1981
Scarid and siganid fishes	*Enhalus acoroides, Thalassia hemprichii, Halodule uninervis, Cymodocea rotundata, Syringodium isoetifolium.* Palau, Western Carolina Islands. Field based monitoring.	All samples of *Thalassia* and *Cymodocea* had bite marks. At one site approximately 30–40% of leaves of all species except *Enhalus*, had at least one bite taken. *Enhalus* had marks on at least 75% of blades.	Ogden and Ogden 1982

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Table 1. (Cont.)

Grazer	Seagrass, location, study type	Description of results	References
Trichechus manatus (M)	*Syringodium filiforme*, Cape Canaveral Florida. Field experimentation. Percent cover and aboveground biomass used to document herbivore impact on seagrass.	Grazing led to significant reductions in coverage and biomass and leaf lengths of seagrass. Manatees were highly aggregated but their distribution was positively correlated with the *Syringodium* and *Halodule* density.	Provancha and Hall 1991
Dugong dugong (M)	*Halodule uninervis*, Nang Bay, Moluccas, East Indonesia. Observation and biomass monitoring.	Dugongs were found to remove some 75% of the belowground biomass in the upper 4–5 cm of sediment. Vegetation biomass recovered to nearby ambient levels in just 4–5 months following grazing during the wet season, no such recovery was noted during the dry season.	de Iongh et al. 1995
Dugong dugong (M)	*Zostera capricorni*, *Halophila ovalis* and *Halodule uninervis*. Moreton Bay, east Australia. Aerial and boat surveys, monitoring along with field experiments used to document dugong grazing on seagrass habitats.	Dugongs appear to spend most of their time grazing. In one area, shoot density, above- and belowground biomass were reduced by 65, 73 and 31% respectively over 3.5 months. Grazing impacts were variable, in one area shoot density was reduced by 85% in 12 days, 95% in 17. In another area biomass was reduced by 96 aboveground and 71% belowground.	Preen 1995
Chelonia mydas (R)	*Thalassia testudinum*. Great Iguana, Bahamas. Field based observations and bioenergetic study. A 3 hectare area of turtlegrass was impounded along with 12 turtles and changes in seagrass biomass were noted.	Turtles grazed grass blades by biting the lower parts of the leaves and allowing the upper portion to float away, creating a patch of closely cropped patches with leaves averaging 2.5 cm in length. The grazed areas were recropped while adjacent stands of tall blades remained untouched. There were no sharp boundaries between grazed and ungrazed areas.	Bjorndal 1980
Diadema antillarum (U), and *Chelonia mydas* (R)	*Thalassia testudinum*. St; Croix, USVI. Field experiments where changes in seagrass growth and biomass were recorded along a grazing gradient.	Turtle grazing had a significant negative impact on seagrass production. Urchins were ineffective in controlling the abundance of seagrass. However, urchin grazing did increase the rate at which seagrass biomass turned over with enclosures.	Zieman et al. 1984

seagrass growth or biomass. Still fewer have directly estimated seagrass consumption by herbivores in the field. Of these, even fewer have included estimates of grazer-induced changes in seagrass leaf turnover rates, which, when unaccounted for, can lead to significant underestimates of the amount of seagrass production consumed by herbivores and the degree to which these consumers can impact seagrass density (cf. Sand Jensen et al. 1994; Zieman et al. 1984; Valentine et al. 1997, 2000). In the next section we discuss the limited data in detail.

D. Evidence for Direct Grazing Impacts on Seagrasses

A combination of field observations and short-term experiments show that the variegated sea urchin, *Lytechinus variegatus* (Lamarck), can consume from 50 to 100% of aboveground seagrass biomass produced in some areas of the eastern Gulf of Mexico and Caribbean Sea (Moore et al. 1963; Camp et al. 1973; Greenway 1976, 1995; Zimmerman and Livingston 1976; Bach 1979; Valentine and Heck 1991; Heck and Valentine 1995; Rose et al. 1999). At densities of 10 inds/m^2, *L. variegatus* can reduce turtlegrass habitats to barren unvegetated substrates from fall through early spring (Valentine and Heck 1991). If grazing is persistent throughout the winter and spring, sea urchins can reduce these vegetated habitats to permanently barren unvegetated substrates (Heck and Valentine 1995). In summer, turtlegrass persists under severe grazing pressure and regrows to levels that either equal or exceed the standing crop of nearby ungrazed turtlegrass. The apparent mechanism by which turtlegrass overcomes the effects of this grazing is to increase the production or recruitment of new shoots in the grazed area rather than to increase the production of existing shoots (Valentine et al. 1997). Similarly, the sea urchins *Tripneustes ventricosus* and *Diadema antillarum* can, and the latter did until recently, consume large quantities of seagrass in some Caribbean settings (e.g. Ogden et al. 1973; Lilly 1975; Vicente and Rivera 1982; Keller 1983; Edmunds and Carpenter 2001). Although it was once thought that grazing on seagrasses was predominantly a Caribbean phenomenon (Ogden and Zieman 1977; Ogden 1980; Ogden and Ogden 1982), observations elsewhere show that sea urchins also consume significant amounts of seagrass in eastern temperate North Atlantic, and the tropical Pacific and Indian Oceans (Bak and Nojima 1980; Kirkman and Young 1981; Hulings and Kirkman 1982; Verlaque and Nedelec 1983; Jafari and Mahasneh 1984; Larkum and West 1990; Klumpp et al. 1993; Jernakoff et al. 1996; Alcoverra and Mariani 2002).

In tropical settings where fishing pressure is low, herbivorous fishes, not sea urchins, are the dominant herbivores (e.g. Ogden 1976, 1980; Hay 1981, 1984a; Carpenter 1986; but see Jackson 1997; Lessios, et al. 2001). More than 30 species of Caribbean fishes, predominantly parrotfishes and surgeonfishes, have been found to have seagrasses in their guts (Randall 1967; McAfee and Morgan 1996; Lewis and Wainwright 1985; but see Hay1984a). New evidence indicates that herbivorous fishes can feed extensively on seagrass production in some areas of the Indo-Pacific Ocean as well (Blaber and Blaber 1980; Klumpp and Nichols 1983a,b; Nichols et al. 1986; Mariani and Alcoverra 2000). It is likely that even more species draw nutrition from these plants, as investigators have typically considered the presence of seagrass leaves in the guts of fishes to be incidental intake associated with the capture of animal prey (e.g. Thompson 1959; Carr and Adams 1973; Bell et al. 1978). When seagrass leaves have been isotopically labeled, or fishes have been presented with seagrass in laboratory studies, it has been found that seagrass leaves can contribute to fish growth (e.g. Conacher et al. 1979; Montgomery and Targett 1992). Using stable isotopes, Fry et al. (1982) found that seagrasses and benthic algae contributed significantly to the diets of many fishes in the seagrass beds of St. Croix, USVI. Fry and Parker (1979) also found that seagrasses and other benthic plants contributed significantly to the diets of shrimps and fishes in some areas of Texas. Similarly, Connolly (2003), using stable isotope comparisons among selected fishes and the potential basal sources of food, found clear evidence of a seagrass signature in the tissues of the snub nosed garfish (*Arrhamphus sclerolepis*).

A conspicuous feature of many tropical reefs is the bare-sand "halos" created around reefs; intense fish grazing on sediment bottoms accessible from the reef's shelter prevent seagrasses from growing in these areas (e.g. Randall 1965; Ogden and Zieman 1977; Hay 1984a; McAfee and Morgan 1996). Not all foraging in and on seagrasses is limited to the base of coral reefs, however (Ogden and Zieman 1977). While many herbivorous fishes seek shelter on coral reefs at night, they commonly forage in nearby seagrass habitats throughout the day (Randall 1965;

Ogden and Zieman 1977; Zieman et al. 1984; McAfee and Morgan 1996; but see Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2003). For example, the parrotfish *Scarus guacamaia* and *S. coelestinus* have been reported to move up to 500m inshore from coral reefs to feed (Winn and Bardach 1960; Winn et al. 1964). Away from reefs, juvenile and smaller species parrotfishes also feed on seagrasses (Ogden and Zieman 1977; Handley 1984; MacIntyre et al. 1987; McGlathery 1995; McAfee and Morgan 1996; Kirsch et al. 2002). Once large enough, many of these juvenile fish abandon structurally simpler seagrass habitats for more structurally complex coral reefs where they appear to find protection from large piscivorous fishes (Springer and McErlean 1962; Ogden and Zieman 1977; Dubin and Baker 1982; Handley 1984; Carpenter 1986; Nagelkerken et al. 2001, 2002; Cocheret de la Morinière et al. 2003). These observations suggest that the flow of energy from seagrass habitats to coral reefs can be substantial, but quantitative estimates are constrained by the limited amount of information on food webs of coral reefs (cf. Polunin 1996).

Investigators have used tethering, stable isotope, gut content, and reconstructive sampling techniques to show that seagrasses are readily consumed by fishes, at times in large quantities, in some areas of the Mediterranean Sea, the Indian and Pacific Oceans (Kirkman and Reid 1979, Klumpp and Nichols 1983a, b; Hay 1981, 1984a,b; Lewis 1985; Nichols et al. 1985; Nojima and Mukai 1990; Cebrian et al. 1996a,b; Pinto and Punchihewa 1996; Marguiller et al. 1997). In virtually every study that offered seagrass leaves to consumers, they were readily consumed by herbivores, thereby demonstrating the susceptibility of seagrasses to herbivores across broad geographic areas.

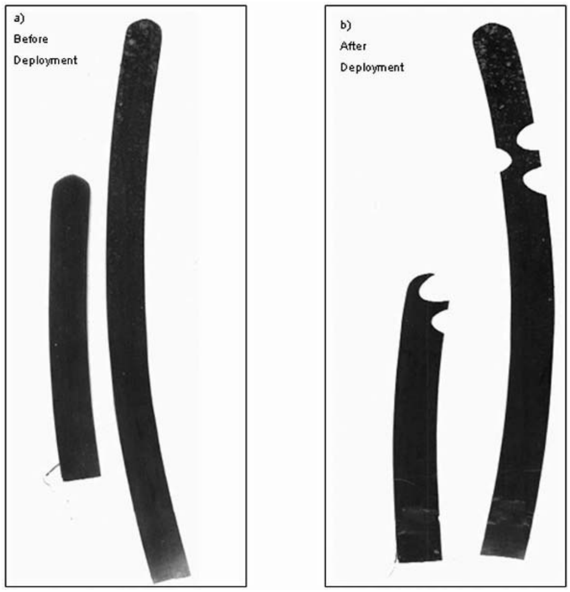

Fig. 4. Digital images of tethered turtlegrass (*Thalassia testudinum*) leaves a) before and b) after deployment in the field for 24 hours (Kirsch et al. 2002).

Of all of these studies, only one has directly estimated the proportion of seagrass production consumed by herbivorous fishes in the field. In that study, Kirsch et al. (2002) used a digital scanner and commercially available software to estimate directly the amount of turtlegrass tissue lost to smaller parrotfishes (*Sparisoma radians*) on a daily basis in the northern Florida Keys (Fig. 4). The areal losses of leaf tissue to these small herbivores were then compared with the amount of leaf tissue produced daily. From these efforts, Kirsch et al. (2002) found that, on average, these fishes consumed some 80% of net aboveground production. While the data indicated that the intensity of this grazing varied greatly among sites, seasons and years, there was no evidence that the variability of grazing was related to the C/N ratios of the leaves. These fishes in turn are readily consumed by a number of piscivorous fishes, thus providing a trophic intermediate for the transfer of seagrass production to the upper levels of marine food webs (Randall 1967; Clifton and Robertson 1993). Taken together, these data show a clear example of an important pathway by which seagrass production can reach higher order consumers.

We have so far emphasized the importance of sea urchin and fish grazing on seagrasses, but it should also be noted that several species of waterfowl have been shown to consume large quantities of seagrass production (both above- and below-ground) during their seasonal migrations through subtropical, temperate and boreal estuaries (e.g. Charman 1977; Wilkins 1982; Tubbs and Tubbs 1983; Baldwin and Lovvorn 1994; Michot and Chadwick 1994; Mitchell et al. 1994; Ganter 2000). In addition, green turtles (*Chelonia mydas*) and sirenians (manatees and dugongs), feed intensely on seagrasses in areas where they are still abundant (Heinsohn and Birch 1972; Lipkin 1975; Spain and Heinsohn 1973; Heinsohn et al. 1976; Anderson and Birtles 1978; Nietschmann and Nietschmann 1981; Marsh et al. 1982; Ogden et al. 1983; Nishiwaki and Marsh 1985;

Lanyon et al. 1989; Nietschmann 1990; Provancha and Hall 1991; Preen 1995). These large herbivores can have even greater impacts on seagrass productivity and abundance than sea urchins or fishes (Zieman et al. 1984). All of these examples suggest that seagrass herbivory, although reduced in an historical context, can represent an important and underestimated trophic pathway in many areas today, rather than a highly localized anomalous event.

E. Dynamic Seagrass Responses can Lead to Underestimates of Grazing Losses

Ecologists have long known that multiple factors can determine the rate at which plants recover following bouts of grazing. Recognizing this, aquatic and terrestrial ecologists have employed increasingly sophisticated field manipulations of nutrients, grazers, light and their interactions (see recent reviews by Vanni 1987b; Athey and Connor 1989; Neckles et al. 1993; Rosemond et al. 1993) to identify the dynamic nature of interactions between grazers and their forage. Based on such studies in marine and other ecosystems, we know that plants can compensate for losses to grazers via either enhanced growth, increasing nutrient uptake from the surrounding environment (Lehman and Scavia 1982; Cargill and Jeffries 1984; Bianchi 1988; Williams and Carpenter 1988; Seagle et al. 1992; Sand-Jensen et al. 1994; McNaughton et al. 1996) or translocating nutrients among physiologically integrated ramets (Jónsdóttir and Callaghan 1990). Yet the mechanisms by which seagrasses respond to herbivory remain inadequately studied.

Unlike many species of marine macroalgae and phytoplankton that are wholly exposed to marine grazers and often totally consumed by them (cf. Hay and Steinberg 1992; Steneck and Dethier 1994), the stored reserves and sites of nutrient uptake for many seagrasses are located in a belowground refuge which is not readily accessible to most grazers. This belowground refuge represents a stabilizing influence that allows seagrasses to persist where herbivory is intense and can, depending on the season, allow seagrasses to recover rapidly to pre-grazing levels (Valentine and Heck 1999).

Many of the early estimates of grazing on seagrasses were based on simple comparisons of aboveground biomass in grazed and ungrazed areas. From these studies it has been indirectly estimated that, depending on site, somewhere between $\sim$3% and 100% of seagrass net primary production enters food webs via the grazing pathway. Most of such studies relied on short-term laboratory measurements or anecdotal field observations to identify the levels of seagrass production entering local food webs. Such calculations do not account for the possibility that grazing stimulates production (e.g. McNaughton et al. 1996), such that rates of aboveground seagrass production (via either increased production by surviving shoots or via the increased recruitment of new shoots) following grazing could exceed those occurring in ungrazed areas. It is likely that this resulted in large underestimates of the amount of seagrass production reaching higher-level consumers via the grazing pathway (Kirsch et al. 2002). This enhanced production following grazing has been recognized as significant in many ecosystems (Lehman and Scavia 1982; Cargill and Jeffries 1984; Bianchi 1988; Williams and Carpenter 1988; Littler et al. 1995; McNaughton et al. 1996), and more recently has been shown to be substantial in seagrass ecosystems (Valentine et al. 1997, 2000; Valentine and Heck 2001). Since new shoots are produced predominantly at rhizome apices (Tomlinson and Vargo 1966), it is reasonable to expect that grazing should also lead to increased belowground production (Valentine et al. 1997). And while we need to develop a better understanding of the role of sediment porewater nutrient concentrations and rhizome carbohydrate stores in determining seagrass responses to grazing (cf. Zieman et al. 1984; Valentine et al. 1997; Valentine and Heck 1999), there have been no such sustained experiments that have simultaneously considered the roles of each of these factors, how they could be influenced by herbivory, or what impact they may have on the transfer of energy within nearshore food webs. Thus, the evidence suggests that the grazing of seagrasses often has been underestimated due to methodological artifacts.

F. Factors that Influence Temporal and Geographic Variability of Seagrass Herbivory

Spatial and temporal variation in herbivory among individual plants is one of the most consistent yet poorly understood aspects of plant-animal interactions (cf. Louda and Collinge 1992; Hacker and Bertness 1995, 1996). While many explanations have been advanced to explain why herbivores exhibit such a discriminating palate, differences in nutritional quality among individual plants appear to be of central importance (cf. Hunter and Price 1992; Hacker and Bertness 1995, 1996). Plant nutritional quality, often expressed as leaf nitrogen content, plays a central role in determining the feeding patterns of a diverse array of terrestrial herbivores (e.g., Onuf et al. 1977; Slansky and Feeny 1977; Kraft and Denno 1982; Coley 1983) that preferentially graze on the leaves of nitrogen-rich plants (e.g. McNeill and Southwood 1978; Schroeder 1986; Athey and Connor 1989). By feeding on nitrogen-rich leaves, herbivores often realize higher survivorship, faster growth, and higher levels of fecundity (e.g. Feeny 1970; Scriber and Feeny 1977; Rausher 1981; Raupp and Denno 1983; Schroeder 1986). These findings have led some investigators to hypothesize that low leaf nitrogen concentration (not C/N ratio) represents one form of plant defense against grazing by specialist herbivores (Feeny 1970; Schroeder 1986; Augner 1995).

Some herbivores, however, have adapted to living in a world dominated by plants of limited nutritional content (e.g. McGinnis and Kasting 1967; Mattson 1980; Lincoln et al. 1982; Strong et al. 1984; Slansky and Scriber 1985; Terra et al. 1987; Simpson and Simpson 1990; Slansky 1993). These adaptations include increasing the length of feeding bouts and/or increasing rates of consumption to compensate for shortages in the nitrogen content of the available forage (Mattson 1980; Moran and Hamilton 1980; Price et al. 1980; Clancy and Feeny 1987). Therefore, low nutritive value, by itself, is not a universally effective defense against grazing (cf. Boyd and Goodyear 1971; Mattson 1980; Moran and Hamilton 1980).

Compared to the well-studied role of terrestrial plant nitrogen content on herbivore food selection, the impact of seagrass leaf nutritional quality (in the case both leaf nitrogen content and the seeming indigestibility of leaf carbon) in determining food selection in seagrass-dominated ecosystems remains inadequately investigated. This issue is significant, given that most marine consumers appear to be broad generalists, i.e. most feed on a range of primary producer taxa. Several correlative field studies have found a significant, positive relationship between leaf nitrogen content and grazing by vertebrates, whether parrotfishes, sea turtles, or dugongs (Bjorndal 1980; Zieman et al. 1984; McGlathery 1995; Preen 1995, but see Cebrián and Duarte 1998). There are no rigorous studies of the importance of diet mixing in determining foraging strategies of seagrass-associated herbivores (e.g. Cruz-Rivera and Hay 2000), despite the domination of marine herbivore guilds by generalist grazers. Given the diversity of epiphytic algae in many seagrass beds, it seems likely that leaf epiphyte composition, which can range from nutritious diatoms and fleshy green algae to grazer-resistant calcareous algae (Klumpp et al. 1993; Heck et al. 2000), will interact with seagrass leaf nitrogen content to influence herbivore foraging choices.

As mentioned above very few studies have experimentally investigated the relationship between grazing intensity and nitrogen concentration of seagrass leaves. Instead studies have relied on comparisons of published proportional differences in the C/N ratios of seagrass leaves and macroalgae to explain why herbivores avoid feeding on seagrass leaves (see Lodge 1991). Yet when detailed comparisons of absolute nitrogen content are made between algae and vascular macrophytes, the differences tend to be quite small (Lobel and Ogden 1981; Lowe and Lawrence 1976; Thayer et al. 1984; Lodge 1991; Strong 1992; Pillans et al. 2004). So it seems likely that factors other then the nitrogen content of leaves are responsible for the relatively low levels of grazing on seagrass leaves. When controlled preference tests, which include both macroalgae and seagrasses, have been conducted, seagrass leaves have been found to be of intermediate palatability in grazer-rich environments (Hay 1984a). Surprisingly, little consideration has been assigned to what role chemical feeding deterrents present in these same nitrogen-rich macroalgae might make in leading herbivores to feed on seagrasses. The importance of chemical deterrents in influencing herbivore food choice are now well documented in coral-reef and many other marine ecosystems (e.g. Hay and Steinberg 1992). Similar studies have not yet been conducted in areas with high seagrass species richness.

Another intriguing consideration in evaluating grazing impacts on seagrasses is that some larger grazers appear capable of managing the nutritional content of their forage through repetitive grazing. Using comparisons between grazer exclusion cages and varying degrees of mechanical simulations of dugong grazing in nearby open areas, Preen (1995) inferred that dugongs were cultivating the nutritional condition of their feeding grounds by preventing fibrous, low nitrogen *Zostera capricorni* from dominating the submerged landscape. Instead the disturbance of the sediments by dugong feeding was hypothesized to allow their preferred forage, *Halophila ovalis*, a rapidly growing less fibrous plant with higher nitrogen content in leaves, to persist in their foraging grounds (Preen 1995). Similarly, it has been suggested that green turtles can cultivate the nitrogen content of their forage by pruning away older more fibrous turtlegrass leaves, allowing them access to a greater abundance of younger more nitrogen rich leaves (Bjorndal 1980).

Of course, not all herbivores, in particular smaller and more sluggish herbivores, have the ability to manipulate the nitrogen content of seagrass leaves. As a result, such organisms may need to find other ways to compensate for the low nutritional quality of their forage, such as compensatory feeding. In the only experimental study we know of where the possibility of such compensatory feeding on seagrasses has been considered, Valentine and Heck (2001) manipulated the *in situ* nitrogen content of seagrass leaves within cages where urchins (*Lytechinus variegatus*) were stocked at densities ranging from 0-20 individuals per square meter of seagrass habitat. The authors found a clear disconnect between the impacts of these grazers on seagrass density and the proportion of seagrass production they consumed. Because the grazers stimulated above-ground seagrass production within the unenriched urchin enclosure cages, the anticipated differences in above-ground seagrass biomass between nitrogen-enriched and unenriched urchin enclosure treatments were not observed. Relying instead on a mass balance estimate of urchin consumption in the nitrogen-enriched and unenriched cages, and on estimates of urchin consumption of nitrogen-enriched and unenriched seagrass leaves embedded in agar, the authors found that urchins would increase the consumption of leaves with low nitrogen to meet their nutritional needs.

Because several generalist herbivores increase their ingestion rates when feeding on marine plants of low nutritional value (Lares and McClintock 1991), it seems likely that many invertebrate grazers may be able to compensate for low nutritional quality of their forage as well. Similarly, most herbivorous fishes have high consumption rates and rapid gut throughput times (Horn 1989). These fishes can maintain very large populations and high growth rates on diets low in protein (Russ 1984; Russ and St. John 1988). Thus, they must process a great deal of organic material very quickly and could consume significant quantities of seagrass production when herbivore biomass is high. Therefore, we believe that it is premature at this stage to draw firm conclusions about how important the variability of the nutritional content of seagrass is in determining herbivore feeding choices. Clearly additional study is needed.

There is new experimental evidence that at least some herbivores will preferentially feed on nitrogen-rich plants in seagrass ecosystems. Goecker et al. (2005) conducted a series of controlled choice tests designed to assess the degree to which one abundant specialist seagrass herbivore (*Sparisoma radians*) would selectively forage on seagrass leaves of differing nitrogen content. Seagrass leaves of varying leaf nitrogen content were offered on paired tethers placed at multiple locations over two seasons in the lower Florida Keys. The results of this comparison were surprising in that the bucktooth consumed virtually all of the enriched leaves while eating minimal amounts of low nitrogen leaves. Because there was concern that the high nitrogen leaves might represent novel prey, as there were differences in the color of the high and low nitrogen leaves, a second set of experiments were conducted in a laboratory setting. This time the leaves were dried and embedded in agar. The results were similar; these small parrotfish consumed substantially more of the agar that was impregnated with the high nitrogen leaves. These findings suggest an interesting and as yet unconsidered possibility, the perceived poor nutritional content of seagrass leaves in the field may in some instances result from preferential removal by herbivores of nitrogen-rich leaves, rather than from limited concentrations of nitrogen in nearshore waters.

There are, of course, many factors other than nutritional or chemical quality of the food that influence herbivore feeding. Chief among these are interactions between herbivores and other animals, including competitors and especially predators. We return to the role of such food-web interactions below.

VI. Indirect Effects of Grazing on Seagrass Communities: A Delicate Balance

Evidence presented in the preceding sections suggests that direct grazing on modern seagrasses may be more common than has been assumed. Nevertheless, there are large regions of the world, particularly in temperate regions, where such grazing is now extremely episodic, negligible, or absent. In such places, the dominant primary consumers are mesograzers—small grazing and detritivorous invertebrates, primarily amphipod, and isopod crustaceans, hermit crabs, and gastropod molluscs (Orth and van Montfrans 1984; Klumpp et al. 1989; Brawley 1992; Jernakoff et al. 1996; Heck et al. 2000). Beds of seagrasses and benthic algae throughout the world typically harbor dense populations of these mesograzers. Estimates based on their consumption and secondary production rates, as well as a limited number of experimental studies (see below), suggest that mesograzers play pivotal roles in marine benthic communities, both in transfer of primary production to higher trophic levels, including fisheries (Kikuchi 1974; Klumpp et al. 1989; Edgar and Shaw 1995; Taylor 1998), and in structuring the assemblages of plants on which they feed (Orth and van Montfrans 1984; Hootsmans and Vermaat 1985; Short et al. 1995; Williams and Ruckleshaus 1993; Jernakoff et al. 1996; Duffy and Hay 2000; Duffy and Harvilicz 2001; Duffy et al. 2001, 2003).

Of particular interest in the context of seagrass ecosystems is the potentially central role of mesograzers as ecological engineers (*sensu* Jones et al. 1994), specifically in indirectly facilitating seagrass dominance by cropping epiphytic algae that would otherwise outcompete the seagrasses for light and water-column nutrients. Numerous lab and microcosm studies have documented that—with some important exceptions—the majority of small grazing invertebrates associated with marine plants feed preferentially or exclusively on benthic algae and detritus, and little if at all on seagrasses (reviewed by Orth and van Montfrans 1984; van Montfrans et al. 1984; Klumpp et al. 1989; Brawley 1992; Jernakoff et al. 1996). Because algae generally grow faster than seagrasses, and can grow on the seagrasses themselves, algae are competitively superior to seagrasses under many conditions and can potentially exclude them from well-lit shallow waters when grazing is ineffective (Valiela et al. 1997). Thus, mesograzers potentially form one member of a critical three-way interaction with seagrasses and algae; their preferential grazing on epiphytic algae potentially releases seagrasses from competition, allowing seagrasses and the ecologically and economically important communities that depend on them to flourish. While the general feeding preference of mesograzers for algae is well established, however, direct experimental confirmation that this grazing actually translates into enhanced seagrass performance in the field has proven more difficult (but see Heck et al. 2000). Table 2 summarizes existing evidence from laboratory, mesocosm, and field experiments for mesograzer mediation of plant community structure in seagrass beds. We restricted our consideration to studies of living seagrasses rooted in sediment, and that presented some quantitative measure of the influence of mesograzers relative to treatments in which mesograzer abundance was experimentally reduced. The collective weight of these few experiments demonstrates convincingly that natural densities of small crustaceans and gastropods greatly reduce the accumulation of epiphytic algae on macrophytes, and suggests strongly, although indirectly, that exclusion of grazers often has serious negative consequences for seagrass growth, biomass, and cover.

Despite the clear potential for mesograzers to facilitate seagrass dominance, however, the existing data have several significant limitations. First, empirical evidence for such facilitation, particularly by crustaceans, comes largely from short-term, small-scale laboratory and mesocosm experiments. Many experimental studies of seagrass-mesograzer interactions, particularly the early pioneering ones, were unreplicated or pseudoreplicated, conducted under artificial conditions, and/or of short duration (Table 2). For example, many early experiments were conducted in aquaria in the laboratory, or with seagrasses planted in submerged flower pots. These designs are understandable, given the logistical challenges of working in the field with clonal plants rooted in sediments and manipulating abundances of very small animals with rapid population growth rates. However, such experiments are probably unable to detect the potentially important effects of physiological integration among seagrass ramets growing in large beds (Valentine et al. 2004), or the interactions between grazing and the often widely fluctuating environmental conditions characteristic of estuaries and coastal environments. Nonetheless, replicated experiments conducted in the field (Robertson and Mann 1982; Phillipart 1995; Fong et al. 2000; Schanz et al. 2002) and in outdoor mesocosms (Howard and Short 1986; Duffy et al. 2001, 2003) support earlier results showing that gastropod and crustacean mesograzers are essential to healthy seagrass stands. Exclusion of these grazers often increases biomass of epiphytes and other fouling material (including attached or sessile invertebrates) by an order of magnitude, and reduced seagrass biomass or cover by 50% or more (Table 2). Thus, the general picture emerging from experimental studies is that

Table 2. Summary of experimental studies measuring direct and indirect impacts of mesograzers on primary producers in seagrass beds. Updated in part from van Montfrans et al. (1984) and Jernakoff et al. (1996). (A) = amphipod; (G) = gastropod; (I) = isopod; (C) = caridean shrimp. The table includes only experiments using live, rooted seagrass, and reporting quantitative measures of grazer effects relative to treatments with grazers excluded or reduced.

Grazers	Seagrass, location, study type	Major results	Reference
Littorina neglecta (G)	*Zostera marina*. Chezzetcook Inlet, Nova Scotia, Canada. Field, 26 days.	Grazer exclusion produced ‘extremely large’ (∼50-fold) periphyton accumulation.	Robertson and Mann 1982
Hydrobia ulvae (G), *Littorina littorea* (G), *Idotea chelipes* (I)	*Zostera marina*. SW Netherlands. Laboratory, 14 days.	Grazers reduced algal mass by 51–81% depending on species; enhanced seagrass growth by 22–71%.	Hootsmans and Vermaat 1985
Natural, mixed-species assemblage of 12 crustacean and gastropod species	*Halodule wrightii*. Indian River Lagoon, Florida, USA. Outdoor mesocosm, pseudoreplicated, ∼90 days.	Grazer exclusion appeared to increase epiphyte mass, increase seagrass defoliation, and reduce seagrass growth.	Howard and Short 1986
Mixed-species assemblage of 6 isopod and gastropod species	*Zostera marina*. Roskilde Fjord, Denmark. Field, unreplicated, 7 days	Grazers reduced algal mass by 60%.	Borum 1987
Idotea resicata (I)	*Zostera marina*. Washington, USA. Laboratory, unreplicated, ∼42 days.	*I. resecata* reduced epiphyte mass by 67%, enhanced seagrass growth by 8–33%	Williams and Ruckelshaus 1993
Mixed-species assemblage of 6 isopod, amphipod, and gastropod species	*Zostera marina*. Chesapeake Bay, Virginia, USA. Glasshouse microcosms, 4 experiments, ≤65 days.	Grazer exclusion increased epiphyte mass up to ∼10-fold, reduced leaf biomass production by up to ∼90%. Grazers promoted cyanobacteria over diatoms.	Neckles et al. 1993, 1994
Hydrobia ulvae (G)	*Zostera noltii.* Wadden Sea, Netherlands. Field, 54 days.	∼50% reduction in grazer mass doubled periphyton mass; decreased seagrass shoot density by ∼1/4, total eelgrass mass by ∼1/2. Snails reached larger sizes at lower density, implying reduced competition for food.	Philipart 1995
Thalotia conica (G), mixed-species assemblage of crustaceans	*Posidonia sinuosa*. Western Australia. Field, 35 days.	Grazers reduced epiphyte mass by 44%. Effects on seagrass complicated by experimental artifacts.	Jernakoff and Nielsen 1997
Clithon spp. (G)	*Zostera japonica*. NE Hong Kong. Field, 120 days.	Grazer exclusion increased periphyton mass by >300%, decreased seagrass % cover by >1/2.	Fong et al. 2000
Gammarus mucronatus (G), *Idotea baltica* (I), *Erichsonella attenuata* (I), alone and in combination	*Zostera marina*. Chesapeake Bay, Virginia, USA. Outdoor mesocosms, ∼42 days.	All grazers reduced periphyton mass by ∼2/3; grazer impacts on seagrass mass ranged from +200% (*Erichsonella*) to −38% (*Idotea*).	Duffy et al. 2001
Gammarus mucronatus (G), *Cymadusa compta* (A), *Ampithoe longimana* (A), alone and in combination	*Zostera marina*. Chesapeake Bay, Virginia, USA. Outdoor microcosms, ∼28 days.	Grazer exclusion increased mass of epiphytes by >10-fold, increased mass of fouling tunicates; grazers did not affect seagrass mass in this late summer experiment.	Duffy and Harvilicz 2001
Hydrobia ulvae (G)	*Zostera noltii*. Wadden See, Germany. Field, ∼28 days.	Transplantation of fouled seagrass to area with grazers reduced epiphyte mass by ∼10-fold. Snail density, and consequently grazing impact, appeared to be controlled by hydrodynamics.	Schanz et al. 2002
Six species of crustaceans and gastropods, alone and in combination	*Zostera marina*. Chesapeake Bay, Virginia, USA. Outdoor mesocosms, ∼42 days.	Grazers reduced algal mass by 21–100% depending on species; grazer impacts on seagrass mass ranged from +117% (*Erichsonella*) to −48% (*Idotea*).	Duffy et al. 2003

epiphyte cropping by mesograzers is a key process facilitating seagrass dominance in shallow, well-lit waters. Accordingly, mesograzers can be seen as having a facultative mutualistic relationship with seagrasses, removing algal competitors in exchange for a substratum and shelter from predators. This positive indirect effect of small invertebrate grazers on seagrasses sets them apart from the large vertebrate grazers and sea urchins discussed previously.

As in many intimate relationships, the facultative mutualism between mesograzers and seagrasses represents a delicate balance and can easily turn antagonistic. Existing experiments illustrate that certain common mesograzer taxa, notably idoteid isopods and ampithoid amphipods, readily feed on seagrasses in the laboratory and can severely overgraze seagrasses when alternative foods are limiting. Several authors have reported loss of seagrass cultures to grazing amphipods in mesocosms (Kirkman 1978; Short et al. 1995), and controlled mesocosm experiments confirm that, in the absence of control by predators, certain isopods and amphipods can completely denude the substratum of seagrass after eliminating algal food (Duffy et al. 2001, 2003; Fig. 5). These results recall the reports of idoteid isopods or ampithoid amphipods occasionally destroying large stands of macroalgae in the field (Kangas et al. 1982; Haahtela 1984; Tegner and Dayton 1987). Yet overgrazing of seagrasses by mesograzers rarely if ever has been observed in nature. Understanding why this is so represents an important and fundamental frontier for research in seagrass community and ecosystem ecology, as it does for ecology generally (Hairston et al. 1960; Polis 1999).

Thus, two major patterns emerge from our review of mesograzer impacts on seagrass communities. First, mesograzers often have positive indirect effects on seagrasses via cropping of their epiphytic algal competitors, and are very probably critical to the survival and ecological dominance of seagrasses in many systems. Second, and in contrast, certain common mesograzers are capable of inflicting severe damage on seagrasses and macroalgae when they reach high densities and exhaust preferred algal foods. Understanding the factors that hold these opposing tendencies in balance is an important frontier for future ecological research in seagrass and macroalgal (e.g. kelp) beds. Thus, despite two decades of research, the importance of epiphyte grazers in the context of the broader field ecology of seagrass ecosystems, encompassing natural variation in light and nutrient regimes, seasonal phenology of plants and grazers, and interactions with predators, remains almost unexplored. We still have a somewhat simplistic understanding of the ecological roles of mesograzers in seagrass systems.

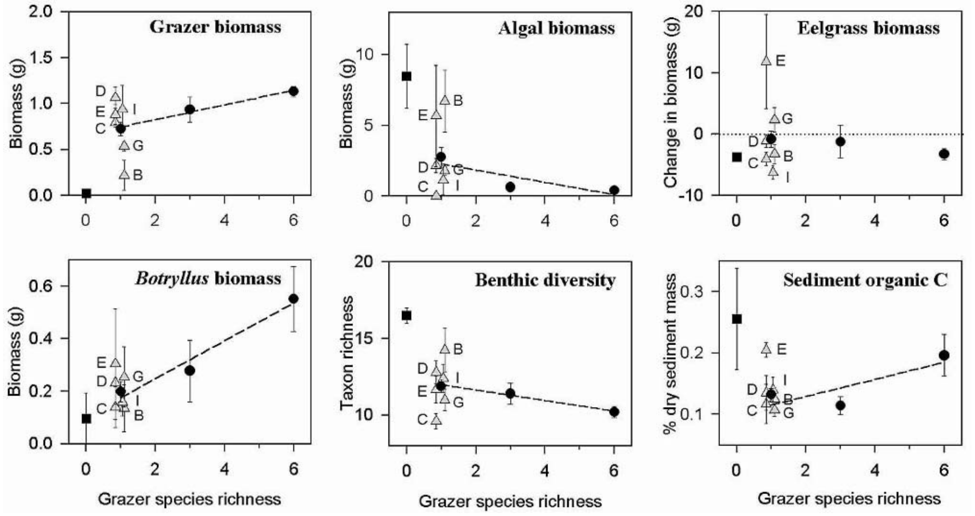

Fig. 5. Effects of mesograzer identity and species diversity on seagrass ecosystem properties after 6 weeks in a mesocosm experiment (Duffy et al. 2003). Squares represent grazer-free controls; circles are means of multi-species grazer treatments; and triangles represent single-species grazer treatments (offset for clarity) identified by first letter of genus name. B = *Bittium varium*, C = *Cymadusa compta*, D = *Dulichiella appendiculata*, E = *Erichsonella attenuata*, G = *Gammarus mucronatus*, I = *Idotea baltica*. *Botryllus schlosseri* is a compound tunicate that encrusts seagrass blades.

This leads us to the broader issue of how grazer populations—and their associated grazing impact—are regulated in seagrass systems.

VII. Bottom-Up and Top-Down Control in Seagrass Communities

Strong (1992) argued that community-wide trophic cascades, in which total plant biomass is strongly reduced, are likely to be most common in low-diversity, algal-based, systems, where single species or functional groups dominate trophic interactions at each level. This entirely plausible suggestion has grown into an article of faith among many ecologists, although it remains largely untested (Duffy 2002). In the context of the present discussion, the important point is that many seagrass systems may approximate the criteria Strong suggested should foster trophic cascades, namely strong trophic interactions among a relatively small number of keystone species or homogeneous functional groups at each trophic level. Thus, first principles might suggest that trophic cascade dynamics may be common in seagrass beds. Alternatively, it might be argued that dominance by vascular plants, rather than by highly edible algae, would foil trophic cascades in seagrass systems. We find this argument unconvincing in light of the repeated observations from lab and mesocosm experiments that certain crustaceans and other animals can greatly reduce seagrass biomass in the absence of predator control. Thus, our specific questions become: (1) what controls grazer biomass and impact under normal circumstances, and (2) what controls seagrass biomass and relative dominance? We must consider the first of these before proceeding to the primary issue of what controls seagrass abundance.

A. Bottom-Up or Top-Down Control of Grazer Populations?

Herbivores are central in food webs both as converters of primary production to a form available to higher-order consumers, and in their important structuring influence on plant communities. As such, the factors regulating herbivore populations are central to understanding dynamics of seagrass (and other) ecosystems more generally. However, determining what controls populations of mesograzers in shallow benthic systems has proven as difficult as the parallel question of what regulates seagrass populations (Heck and Orth 1980; Heck et al. 2000; Williams and Heck 2001; Schanz et al. 2002). A primary reason for this ambiguity is the small sizes and rapid population growth rates of mesograzers, which seriously challenge our ability to conduct the standard field experimental manipulations (e.g. caging) that have proven so successful in understanding the community ecology of larger invertebrates and algae, particularly on hard substrata (e.g. Menge 1995; Bertness et al. 2001).

Historically, the conventional wisdom has held that mesograzer populations are usually controlled by predators, primarily fishes (Nelson 1979, 1981; Heck and Orth 1980; Orth et al. 1984; Duffy and Hay 1991). Several lines of indirect evidence support this view. First, small mobile invertebrates, particularly crustaceans, in the mesograzer size range dominate diets of many nearshore fishes and larger invertebrates (Kikuchi 1974; Adams 1976). Indeed, production of small crustaceans is one of the best predictors of fish production in vegetated marine ecosystems (Edgar and Shaw 1995; Taylor 1998). Moreover, seasonal abundance patterns of fishes and mobile epifauna often show negative covariance (e.g. Nelson 1979; Stoner 1980; Choate and Kingett 1982; Duffy and Hay 1991; Valentine and Heck 1993). These patterns, together with a perceived superabundance of attached microalgae in most seagrass ecosystems, led many researchers to conclude that fish predation regulates mesograzer abundance and by extension grazing pressure in most coastal ecosystems. Despite the circumstantial evidence for predator regulation of epifaunal populations, experimental tests have largely failed to provide definitive support for this hypothesis (references in Edgar 1993). There are several possible methodological reasons for this, including enhancement of mesograzer food and habitat by cage structures, as well as increased predation on mesograzers in predator “exclusion” cages by small decapod crustaceans that often “bloom” or immigrate into cages designed to exclude fishes (Young et al. 1976; Virnstein 1978; Nelson 1981; Olafsson et al. 1994). Moreover, many smaller consumers in seagrass beds are in fact omnivores that feed both on mesograzers and their epiphytic forage (Heck et al. 2000), further complicating the interpretation of the relationship between mesograzer density and grazing intensity. As a result, our understanding of the overall role of top-down control in seagrass beds remains poorly understood.

It is also possible, of course, that the failure to demonstrate predator limitation of mesograzers reflects a true absence of top-down control. To evaluate this possibility, and the relative importance of resource and predator control of mesograzer populations, G.J. Edgar (see below) initiated a series of studies designed to test between them. Experimental manipulations of mesograzer abundance, both enhancement and reduction, in field microcosms (Edgar 1990; Edgar and Aoki 1993) resulted in rapid compensatory responses of the mesograzer assemblage and convergence of estimated secondary production values, consistent with diffuse competition and limitation by a common resource, presumably periphyton production (the "production ceiling" hypothesis, Edgar 1993). These experiments were complemented with field surveys using artificial plants of standardized construction in a wide range of shallow marine habitats and geographic regions to characterize epifaunal assemblages, and relate their characteristics to environmental parameters (Edgar 1993; Edgar and Klumpp 2003). Specifically, abundance and size of epifaunal animals were used to estimate epifaunal biomass and, based on published data on specific production rates, biomass was used to estimate a standardized index of total epifaunal secondary production, P_{20}, representing the aggregate daily secondary production of epifauna normalized to 20° C (Edgar 1993). Surprisingly, P_{20} showed no significant variation among standardized habitats deployed at 17 shallow, clear-water sites worldwide, whereas the index was strongly reduced at deeper, turbid, and nutrient-depleted sites (Edgar 1993), and varied with architecture of the artificial substratum (Edgar and Klumpp 2003). These patterns are consistent with limitation of epifaunal productivity by resources available for primary production (a "production ceiling", Edgar 1993), whereas the lack of variation among sites is unexpected if spatial variation in predation strongly influences epifaunal populations. Thus, the suggestion was that total secondary production of epifauna was regulated by resource availability rather than predation.

The resource ceiling hypothesis and its supporting data are intriguing and potentially quite important. They raise a philosophical question: which aspects of ecological structure and function are we concerned about and why? Although the resource ceiling hypothesis, an explicitly bottom-up hypothesis, appears superficially to be incompatible with hypotheses of predator regulation of epifauna, it is not necessarily so, and focuses attention on the somewhat difficult question of what we mean by "regulation" or "control". The resource ceiling hypothesis suggests that a specific ecosystem-level process, the rate of production of an entire trophic level or functional group, is controlled (limited) by resource availability. Yet the source of this secondary production varies considerably among systems and, in particular, with predator density. In one of the same studies that supported the resource ceiling hypothesis, Edgar and Aoki (1993) showed that fish predation tended to eliminate larger-bodied animals, shifting the epifaunal assemblage toward species resistant to predation, and toward the smallest body-size classes in species vulnerable to predation (e.g., Edgar and Aoki 1993). Thus, both epifaunal demography and species composition changed substantially with predator density despite similar secondary production levels. Such shifts are likely to have profound consequences both for grazer effects on plants, and for the transmission of seagrass epiphytic production to higher trophic levels, including harvested fishes and shellfish. First, recent studies have shown that even superficially similar mesograzer species differ considerably in their grazing rates, food preferences, and per capita impacts on the plant community (Fig. 5; Duffy and Hay 2000; Duffy and Harvilicz 2001; Duffy et al. 2001, 2003). As major macrophyte-grazing taxa tend to be larger-bodied species, which will often be severely reduced by predation, predation on these grazers may cascade down to affect biomass and plant community composition. Second, the similarity of total secondary production estimates between treatments with and without predators presumably does not translate to equivalent secondary production flowing to higher trophic levels, since production by assemblages exposed to fishes is almost entirely due to minute size classes not effectively captured by fishes (Edgar and Aoki 1993). Again, as emphasized by Paine (1980), energy-flow diagrams (including secondary production levels) and community interaction webs for the same community may have quite different appearances.

For mesograzers specifically, this lack of concordance between energetic and interaction estimates of ecological importance has been demonstrated in several experiments. For example, one microcosm experiment compared the grazing impacts and population growth rates of ampithoid amphipods (a mixture of *Ampithoe longimana* and *Cymadusa compta*) and *Gammarus mucronatus* (Duffy and Harvilicz 2001). The two amphipod taxa each essentially eliminated periphyton from eelgrass leaves and reached nearly identical final population biomasses, supporting the general conclusion (Edgar 1993) that a common resource ceiling limited their population sizes and production. Nevertheless, subtle differences in their feeding preferences produced marked differences in the total biomass and composition of the epiphyte community that developed under their influence (Duffy and Harvilicz 2001). In fact, total epiphyte mass in *Gammarus* treatments actually exceeded the fouling mass in grazer-free controls due to *Gammarus* facilitation of the filamentous epiphyte *Polysiphonia* sp., which grew luxuriously only where *Gammarus* was present. A second, similar example comes from a seaweed-dominated system; in this case macroalgal community composition, and particularly biomass of the dominant seaweed *Sargassum filipendula*, differed dramatically between treatments with versus without the herbivorous amphipod *Ampithoe longimana*, despite there being no difference in total epifaunal abundance (nor, presumably, production) among treatments (Duffy and Hay 2000). *Ampithoe longimana* was the only mesograzer that fed significantly on macroalgae in that system. Finally, the frequent destruction of seagrasses by ampithoids and idoteid isopods in predator-free mesocosms (Kirkman 1978; Williams and Ruckelshaus 1993; Short et al. 1995; Duffy et al. 2001, 2003), and similar defoliation of macroalgal beds during occasional amphipod or isopod outbreaks in nature (Kangas et al. 1982; Haahtela 1984; Tegner and Dayton 1987) suggests that some factor other than food availability normally keeps populations of these species in check.

In summary, even if total secondary production is limited by resource availability, as appears true (Edgar 1993; Edgar and Klumpp et al. 2003), predation may remain critical in preventing the explosion of particular keystone or dominant species that could severely damage macrophyte populations and the communities that depend on them. That is, while metabolic rate-based estimates are important indicators of energy flow within ecosystems, they may tell us little about the community-level impacts of grazers (Paine 1980). Realistic experimental tests of the importance of predation in influencing assemblage structure of mesograzers, and their cascading impacts on primary producers in seagrass beds, remain an important challenge for future research.

B. Eutrophication, Overfishing, and the Decline of Estuarine Vegetation

The question of what regulates mesograzer population density and community structure is of far more than academic interest. If mesograzers are as important to facilitating seagrass dominance as existing evidence suggests they are, then any factors—natural or anthropogenic—that affect mesograzer populations may indirectly affect the health of seagrasses. A case in point involves eutrophication, which is a serious threat to seagrass ecosystems worldwide (Short and Wylie-Echeverria 1996; Duarte 2002; Kenworthy et al., Chapter 25). Increased nutrient loading to coastal ecosystems generally favors fast-growing algae over seagrasses, with phytoplankton dominating in deeper basins with low water turnover rate, and benthic algae dominating in shallower basins and where flushing is stronger (Valiela et al. 1997). Thus, dominance by seagrasses is potentially threatened by eutrophication. However, experiments in greenhouses (Neckles et al. 1993), outdoor mesocosms (Lin et al. 1996), and the field (Williams and Ruckelshaus 1993; Heck et al. 2000) have demonstrated that nutrient loading by itself often has little effect on the balance between seagrasses and algae, as long as natural grazer populations are present to crop the algae. Models also predict that natural levels of grazing can often eliminate detrimental effects of nutrient loading on seagrasses (Wetzel and Neckles 1986). These considerations suggest that negative impacts of eutrophication on seagrass ecosystems are more complex than commonly envisaged. Specifically, they suggest that eutrophied systems, which are often impacted by multiple stressors, may degrade as much as a consequence of altered food webs as of nutrient loading by itself (Fig. 6).

A trophic cascade is usually understood to refer to the penetration of predator influence downward through one or more intermediate levels in a food chain to influence plant biomass. Classic examples include the cascading effects of piscivorous fish, through zooplanktivorous fishes and zooplankton, to phytoplankton biomass in northern temperate lakes (Carpenter et al. 1985), and the penetration of killer whale influence, through sea otters and their sea urchin prey, to regulate the abundance and distribution of kelp beds in the northeastern Pacific (Estes and Duggins 1995; Estes et al. 1998). As mentioned above, many seagrass beds, particularly

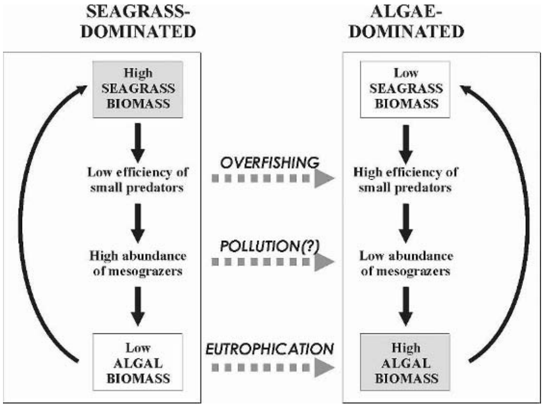

Fig. 6. Hypothesized alternate ecosystem states in well-lit marine and estuarine sediment bottoms. In this hypothesis, both seagrass-dominated and algal-dominated states are maintained by positive feedback loops, mediated by food-web interactions, which render them resistant to perturbation. Once perturbed to the point of state change, however, these positive feedbacks similarly render the system resistant to restoration. Broken arrows denote anthropogenic perturbations impinging at different levels in the food web. Note that all anthropogenic perturbations drive the system in the direction of algal dominance and seagrass decline. See text for details.

in low-diversity temperate estuaries, would appear to be promising candidates for cascading trophic dynamics for several reasons. First, at least in temperate estuaries, diversity is low relative to other systems, suggesting a low potential for compensation among species within trophic levels, and thus stronger propagation of indirect effects from predators to plants. Second, both grazers (Tables 1 & 2) and predators exert strong impacts on plants in seagrass systems. Recent and ongoing experiments provide intriguing preliminary evidence for potential trophic cascades in eelgrass beds of Chesapeake Bay. In this region, decapod crustaceans, including blue crabs (*Callinectes sapidus*) and shrimp (*Palaemonetes* spp.), are among the most abundant predators in seagrass beds. Mesocosm experiments conducted in both fall and spring demonstrated that mesograzer assemblages were strongly depressed by juvenile blue crabs, and that this depression cascaded down to enhance biomass of epiphytic algae (M.S. Harris, J.E. Duffy, and R.N. Lipcius, *unpublished data*). Most intriguingly, addition of a fourth trophic level, in the form of adult blue crabs—which are cannibalistic—reversed these patterns by reducing abundance of juvenile crabs, releasing mesograzers (which adult crabs evidently do not eat effectively) from predation, and again reducing epiphyte biomass. Thus, in these simple mesocosms, adult blue crab addition cascaded through two intermediate trophic levels to reduce algal biomass. On the other hand, arguing against this generality of strong trophic cascades in seagrass beds is the frequency of omnivory among some fishes (e.g. Heck et al. 2000) and decapods, which could foil cascading top-down control. Field-testing the trophic cascade hypothesis in naturally diverse seagrass beds should be a high priority for future research.

This preliminary evidence for cascading effects of predators in seagrass beds recalls the analogous case of salt marshes, where, as in seagrass ecology, a long tradition of research has focused almost exclusively on bottom-up forcing (Silliman and Bortolus 2003). Yet recent experiments in southeastern USA salt marshes show that rasping of the dominant grass *Spartina alterniflora* by abundant littorinid snails can cause severe damage and defoliation, and that snail abundance covaries negatively with predator abundance, suggesting that *Spartina* dominance of intertidal estuaries may depend on a trophic cascade in which predators prevent the overpopulation of grazing snails (Silliman and Bertness 2002). Importantly, as in seagrass systems, the major predators on grazers in salt marshes are commercially harvested species such as the blue crab.

As eutrophication (bottom-up degradation) and overharvesting of fishes and shellfish (top-down forcing) have proceeded simultaneously, the relative importance of these factors to historical degradation of seagrass ecosystems is difficult to disentangle. Doing so will be critical to effective management and mitigation, however. This again focuses attention on the necessity of understanding trophic interactions and their community consequences for effectively managing seagrass ecosystems (Figs. 3 & 6).

VIII. Alternate Stable States in Seagrass Ecosystems?

Integrating the findings of a wide range of studies in seagrass ecosystems, we suggest the hypothesis that shallow sediment bottoms can take one of two alternate ecosystem states (Fig. 6). Healthy seagrass beds are characterized by high seagrass biomass and shoot density, offering effective refuge from predators, thus fostering high abundance and grazing intensity of mesograzers, and low biomass of epiphytes and macroalgae. This seagrass-dominated state is relatively resistant to perturbation. For example, Heck et al. (2000) have shown that high seagrass shoot density can maintain high mesograzer densities, which in turn can control algal biomass accumulation, even under strongly enhanced nutrient loading or enhanced abundance of invertebrate-feeding fishes. Thus, a healthy seagrass bed has some resistance to both eutrophication and the increase in small predator densities that might result from overfishing of large predators.

Well-lit sediment bottoms can also show alternate community state, being dominated by benthic microalgae or macroalgal beds resistant to seagrass encroachment. Under high light and nutrient conditions, algae are inherently competitively superior to seagrasses (Valiela et al. 1997). Thus, once in place, algae are likely to resist the establishment of dense seagrass populations. Moreover, during initial phases of establishment, seagrasses will be patchy and at relatively low shoot density. Many experiments have shown that predators are much more effective in capturing seagrass-associated prey at such low shoot densities. Thus, during early (sparse) seagrass establishment, abundant light in the sparse canopy should favor rapid epiphyte growth and mesograzers should be maintained at low densities by predation (unless associated macroalgae can support a reservoir of mesograzers protected from predation). The low mesograzer densities may act synergistically with the strong light, allowing algal biomass to accumulate.

Thus, a degraded system, with low seagrass and high algal biomass, will tend to resist restoration of seagrasses. It is noteworthy that the several anthropogenic insults common to shallow nearshore systems all would appear to drive this system toward the algal-dominated state, albeit via different points in the cycle (Fig. 6).

IX. Questions and Recommendations for Future Research

A quarter of a century ago, den Hartog (1977) suggested that quantifying effects of grazers on seagrasses should be a "priority desideratum" for future research. Considerable progress has been made in such quantification (Orth and van Montfrans 1984; Jernakoff et al. 1996; Valentine and Heck 1999; Tables 1 & 2), and, despite lingering uncertainty, several converging lines of evidence suggest that top-down forces are likely to play important roles in structuring seagrass communities—in concert with the always important influence of bottom-up processes. This evidence includes the typically strong interactions among consumers and prey in marine systems generally (Cyr and Pace 1993; Menge 1995; Duffy and Hay 2001; Shurin et al. 2002; Fig. 1), the strong grazing pressure, particularly on epiphytes, characteristic of seagrass systems specifically (Tables 1 & 2, Fig. 5), the high abundance of grazers and predators in many seagrass ecosystems (Heck and Orth 1980; Klumpp et al. 1989; Williams and Heck 2001), and the relatively low species diversity of many temperate seagrass ecosystems, which should render trophic cascades more effective (Strong 1992; Duffy 2002). Yet, despite progress, consensus still eludes us regarding the importance of direct grazing on seagrasses, specifically, and the role of consumer control in seagrass communities and ecosystems, more generally.

Uncertainty about the role of consumer control in seagrass ecosystems will be resolved only by rigorous multifaceted field studies that include manipulations of grazing pressure, conducted under realistic conditions and of sufficient duration to detect population- and community-level responses. Central challenges involve scaling up the lab, mesocosm, and small-plot field experiments conducted so far to address processes occurring over larger scales and involving highly mobile consumers. Laboratory and mesocosm experiments, such as those that have dominated seagrass-grazer research to date, have widely recognized limitations (Carpenter 1996; Schindler 1998; Drenner and Mazumder 1999; Huston 1999), and must be interpreted with some caution. It is perhaps less widely recognized—but worth emphasizing—that observational studies and measurements of unmanipulated systems, no matter how long-running or detailed, also have limited ability to identify the causal mechanisms that structure communities (Hairston 1989; Paine 1994). A cautionary example involves the most conspicuous pattern in marine ecology, the sharp zonation of rocky intertidal organisms, which was believed for decades if not centuries to reflect a simple bottom-up mechanism of differential physiological tolerances of species to physical factors. This conventional wisdom proved erroneous when experiments showed that the patterns were strongly controlled by competition and predation (Connell 1961a,b).

A full understanding of any ecosystem thus requires a suite of complementary research approaches. A central point of our contribution is that seagrass ecology would greatly benefit from more rigorous experimental study of food-web interactions. Despite the limitations of existing mesocosm experiments, we are struck by their consistency with one another and with the few field experiments conducted so far. Although they span a wide range of geographic regions, taxa, and designs, most such experiments show that grazers can have strong impacts on the biomass and community composition of primary producers in seagrass beds (Tables 1 & 2). Those grazing impacts are often unrealized in the field, but this does not mean that they are unimportant. Rather, it means that perturbations that change abundance or community composition of grazers, whether large vertebrates or invertebrate mesograzers, could potentially produce strong changes in structure and functioning of seagrass ecosystems. To determine whether and under what circumstances this potential is realized, seagrass ecology needs creative and ambitious efforts to scale up experimental approaches, like those that have proven so successful in research on lake ecosystems (e.g. Carpenter et al. 2001).

In closing, we also wish to emphasize that resolving the role of consumers in seagrass ecosystems is of far more than simply academic interest. Given the accelerating pace of seagrass ecosystem degradation worldwide (Duarte 2002; Kenworthy et al., Chapter 25), understanding the role of community interactions in seagrass systems has increasingly important consequences not only for basic marine ecology but also for conservation and management of these ecologically and economically important resources (Fig. 6). The principal open question for seagrass ecology remains the fundamental one of bottom-up vs top-down control: what are the relative importance of resource supply, consumer pressure, and—most importantly—their interactions, in regulating the performance of seagrasses, and even the existence of seagrass beds? Despite intensive study of seagrass light and nutrient relations on the one hand, and of grazer impacts on seagrasses and epiphytes on the other, there are surprisingly few data available to address their interactions rigorously. Effective management and conservation of seagrass ecosystems will be compromised until we achieve a balanced, empirically based understanding of seagrass-bed interaction webs that incorporates the important functional roles of consumers. We look with hope to the rising generation of students, and we believe the following questions will repay close attention.

How important is top-down control in seagrass ecosystems? The most fundamental question, which feeds into all the others we consider, involves the frequency, magnitude, and nature of consumer impacts in seagrass ecosystems. By top-down control we mean all impacts of consumers on lower trophic levels, including direct grazing on seagrasses, grazing on algae that indirectly influences seagrasses through competitive interactions, and cascading impacts of higher-level predators. Whereas numerous studies have documented impacts of consumers on certain prey populations in seagrass beds, very few have rigorously tested the community- and ecosystem-level consequences of grazing and predation in seagrass systems.

What impact does overharvesting of coastal and estuarine predators have on seagrass systems? Many estuarine predators, such as the blue crab in the southeastern USA, are under heavy fishing pressure. Many such predators are also known or suspected to play important structuring roles in benthic communities, implying that large declines in their abundance may cascade down to affect other levels in the food web (Fig. 3). Such processes have been documented in many other aquatic benthic systems (e.g., Menge 1995; Shurin et al. 2002) but remain mostly untested in seagrass beds (but see Heck et al. 2000 and Gillanders, Chapter 21). Does the removal of large piscivores release herbivores from predator control, resulting in the high estimates of grazing reported above? Or do losses of large predators release smaller predators from control, and thus reduce grazing impact?

To what extent has overharvesting of large vertebrate herbivores and waterfowl reduced the importance of direct grazing on seagrasses in modern food webs? There is strong indirect evidence that reduction of large marine herbivores has reduced direct grazing on tropical seagrasses. But why is there so little direct grazing on temperate seagrasses? Is it possible that the intense hunting of waterfowl has led to a similar reduction in direct grazing on seagrasses in temperate zones as well?

What regulates mesograzer populations and communities? Although this may seem a highly specific problem, it is of central importance to understanding most modern seagrass ecosystems, and to predicting their responses to anthropogenic impacts (Heck et al. 2000). For example, if total mesograzer production, and by inference grazing pressure, is limited by resources (Edgar 1993; Edgar and Aoki 1993; Edgar and Klumpp 2003), then eutrophication may have little impact on epiphyte accumulation on seagrasses as grazer populations respond to the enhanced resource availability. Conversely, if mesograzer grazing pressure is regulated by predation, then grazing is less likely to control epiphytes under elevated nutrient loading. Similarly, overharvesting of top predators should have little effect on seagrass biomass if mesograzers are limited by algal production, but could have important cascading impacts on seagrasses if overharvesting releases lower-level consumers from predatory control.

How does declining biodiversity within seagrass ecosystems affect their structure, functioning, and stability? Functional redundancy among co-occurring species can enhance stability of ecosystem structure and processes (Lawton and Brown 1993; Cottingham et al. 2001), and experiments with synthesized assemblages in several systems have shown that more diverse communities can be more stable in the face of perturbations and natural environmental variation (Mulder et al. 1999; Stachowicz et al. 1999, 2002). Even within a species, genotypic diversity can enhance resistance to perturbation, as shown recently for eelgrass subjected to natural grazing by geese (Hughes and Stachowicz 2004). Continuing loss of species and genetic diversity, e.g., through overharvesting or pollution, might thus render seagrass ecosystems more susceptible to subsequent disturbances.

How will changes in the structure of seagrass and coastal food webs influence the resilience of these systems to excess nutrient loading? This question is related to the previous one. Conservation-oriented seagrass research (see Kenworthy et al., Chapter 25) has understandably focused primarily on detrimental effects of nutrient loading and turbidity, as nutrients and light are easily measured and straightforwardly related to plant growth and competition. But both theory and a growing number of experiments show that seagrass systems can be strongly buffered against effects of nutrient loading as long as a balanced assemblage of mesograzers and predators is present. Thus, an important question for seagrass conservation is how grazer assemblages, and food webs generally, are affected by anthropogenic impacts and how these interact with nutrient loading.

X. Summary

Seagrass food webs contain two key conduits for the transfer of primary production to higher order consumers: (1) *Seagrass grazing ecosystems* are or were characterized by moderate to intense grazing on living seagrass leaves and rhizomes by abundant large vertebrate and some invertebrate herbivores, resulting in low seagrass biomass and direct conversion of much seagrass production into vertebrate biomass; (2) *Seagrass detrital ecosystems* are mostly devoid of large vertebrates, and herbivory is dominated by small invertebrate mesograzers that feed preferentially on epiphytic algae, indirectly enhancing seagrasses, and resulting in high seagrass biomass and most seagrass production entering the detrital food chain. For most of the past 50 My, seagrass food webs, at least in the tropics, were apparently of the former type.

This history has implications for understanding the adaptive significance of characteristic morphological, demographic, and life history traits of seagrasses, many of which—like those of their terrestrial counterparts—may be adaptations to historically chronic grazing. In modern seagrass systems, direct grazing of seagrasses is relatively low on a global average (<30% of production), due in part to overharvesting of vertebrate grazers, but is highly variable in space and time. Thus, many modern seagrass ecosystems are of the detritus-based type, with little seagrass production grazed directly.

An important implication is that the seagrass detrital ecosystems on which most research has focused are an historical anomaly and may have been rare prior to human impact. Moreover, direct grazing of seagrasses remains locally intense in certain regions, both tropical and temperate. Importantly, in both grazing and detrital seagrass ecosystems, grazing is an important controlling influence on seagrass community and ecosystem dynamics, whether through direct consumption of seagrass tissue, or indirectly as algal grazers mediate competitive interactions between seagrasses and algae.

Seagrasses today remain intimately connected with herbivores and predators through food-web linkages. Rigorous understanding of seagrass ecology and responses to anthropogenic change (e.g., eutrophication) thus requires a broadening of the historically dominant bottom-up perspective to include the important structuring roles of consumers. Better understanding and recognition of the importance of

seagrass food-web interactions is critical to effective management of these valuable natural resources.

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Chapter 21

Seagrasses, Fish, and Fisheries

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I. Introduction

Seagrass meadows have extremely high primary and secondary productivity and support a great abundance and diversity of fish and invertebrates. A number of commercially and recreationally important species (including both fish and invertebrates) have been linked to seagrass at some stage of their life cycle, although few such species use seagrass throughout their life. Non-commercial species within seagrass may be an important food source for commercial species (forming trophic linkages). In addition, some species that do not inhabit seagrass may derive benefit from seagrass by way of exported seagrass detritus or resident/transient species that move out of seagrass (some of these topics are dealt with elsewhere in this volume: e.g. Heck and Orth, Chapter 22, Kenworthy et al., Chapter 25 and Bell et al., Chapter 26).

A considerable amount of research on fish and invertebrates within seagrass meadows has been done, including many fisheries-related aspects. Besides individual research papers, a number of reviews on the ecology of fish assemblages and fisheries associated with seagrasses are available (e.g. Bell and Pollard, 1989; Butler and Jernakoff, 1999; Jackson et al., 2001). It is not my intention to duplicate these reviews, but rather report on and synthesize recent research that is contributing to our understanding of the fauna of seagrass meadows. In this chapter, I use the terms fish and fisheries broadly to encompass both fish and invertebrates. I will briefly mention the use of seagrass beds by fish species, which are both temporary and permanent residents, but note that this area has recently been covered in a review by Jackson et al. (2001). I will compare the abundance, diversity, growth, and survival of fish in seagrass meadows with other nearshore habitats, but again point the reader to a series of recent reviews and meta-analyses that critically review the nursery role hypothesis (sensu Beck et al., 2001) by comparing nearshore habitats to seagrass (Heck et al., 2003), marsh (Minello et al., 2003), and mangrove (Sheridan and Hays, 2003) habitats. I will then focus on patterns and potential mechanisms that may contribute to spatial and temporal variation in abundances of fish in seagrass meadows. I will investigate links between seagrass and fisheries with a focus on new methods such as otolith chemistry and stable isotopes for determining such linkages. Finally, I will investigate some of the conservation and management issues that pertain to seagrass habitats in terms of their occupants (e.g. impacts due to fisheries and restoration of seagrass habitats in terms of fish and fisheries).

II. Use of Seagrass Beds by Fish Species

Seagrass meadows provide shelter and food for assemblages of fish. Increased food availability to juveniles and protection from predators are often cited as reasons why such large numbers of organisms are associated with seagrass, but studies that actually evaluate whether more food is available are scarce (Heck et al., 1997). Increased food is thought to lead to increased growth rates, which in turn facilitates lower mortality rates (Bell and Pollard, 1989). The structural complexity of seagrass habitats is also thought to provide shelter from predators. In addition, seagrass beds often are located some distance from reef habitats (rocky reef or coral reef) and offshore waters and therefore may have fewer predators. Some of these issues, such as food vs. protection vs.

A. W. D. Larkum et al. (eds.), Seagrasses: Biology, Ecology and Conservation, pp. 503–536.

other factors are teased out further in Heck and Orth, Chapter 22.

A. Permanent Residents of Seagrass Beds

Few species of fish inhabit seagrass beds all year round and throughout their entire life history. Permanent residents are usually small in size and cryptic (Edgar and Shaw, 1995a). Although the proportion of resident species may represent half of the total number of species present (e.g. Hair et al., 1994), residents are likely to represent less of the total number and/or biomass of individuals. For example, two studies suggest that resident species represent less than 20% of the total number of individuals (Hair et al., 1994; Arrivillaga and Baltz, 1999). To gain a better understanding of the proportion of resident species in terms of both number of species and number of individuals, future studies should report these figures. Resident fish will feed within seagrass beds, but usually not on the seagrass itself. Resident species are also known to spawn in nearshore seagrass areas including species that brood eggs (e.g. syngnathids) or have demersal eggs (e.g. atherinids).

B. Species Utilizing Seagrass on Rare Occasions

A number of species that are abundant on coastal reefs may also occur in low numbers in seagrass beds (Bell and Worthington, 1993). Bell and Worthington (1993) note that from extensive sampling of eelgrass (*Zostera capricorni*) and southern strapweed (*Posidonia australis*) in New South Wales (Australia) most reef species are represented in these estuarine habitats by a total of only 1–10 individuals (sampling comprised $n = 40$, 20 m^2 samples at each of 16 sites spanning 300 km for *Zostera* and $n = 32$, 50 m^2 samples at each of 9 sites spanning 300 km for *Posidonia*) (Fig. 1).

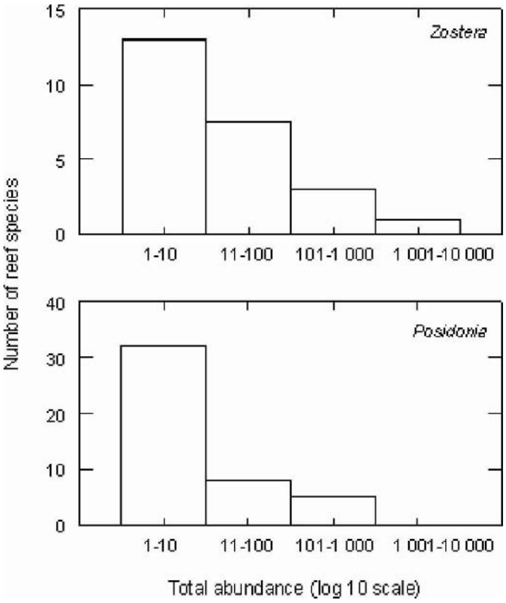

Fig. 1. Distribution of frequencies of log total abundance for reef fish species whose juveniles were found in the seagrasses *Zostera capricorni* ($n = 40$, 20 m^2 samples at each of 16 sites spanning 300 km) and *Posidonia australis* ($n = 32$, 50 m^2 samples at each of 9 sites spanning 300 km) on the New South Wales coast (Australia) between 1988 and 1990. Data from Bell and Worthington (1993), reproduced by permission of NIWA.

C. Temporary Residents of Seagrass Beds

The majority of species only use seagrass for a small part of their life history (i.e. settle there from the plankton and then move to other habitats at larger sizes and ages), as a temporary foraging area or as a temporary refuge from predation (Jackson et al., 2001). Inshore areas in general may provide higher temperatures and increased prey availability, which facilitate rapid growth, but may be important predation refuges as well.

The importance of seagrass beds as ‘nursery’ habitats for commercially important species has reached almost paradigm status, despite few studies mentioning the proportion of fish from seagrass habitats that were early juveniles. In fact, Edgar and Shaw (1995a) found that seagrass beds in Western Port (Victoria, Australia) were not a major habitat for juveniles of economically important species. Other studies have, however, found that most of the fish in seagrass beds were juveniles. For example, in a study of a Guatemalan seagrass bed, 83% of fishes were early juvenile stages (Arrivillaga and Baltz, 1999) and in experiments in Botany Bay (New

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Abbreviations: ASU – artificial seagrass unit; CPUE – catch per unit effort; CWT – coded wire tags; $\delta^{13}C$ – ratio of ^{13}C to ^{12}C based on a belemnite standard; $\delta^{15}N$ – ratio of ^{15}N to ^{14}N; SAV – submerged aquatic vegetation; SRI – seagrass residency index; VIF – visible implant fluorescent elastomer

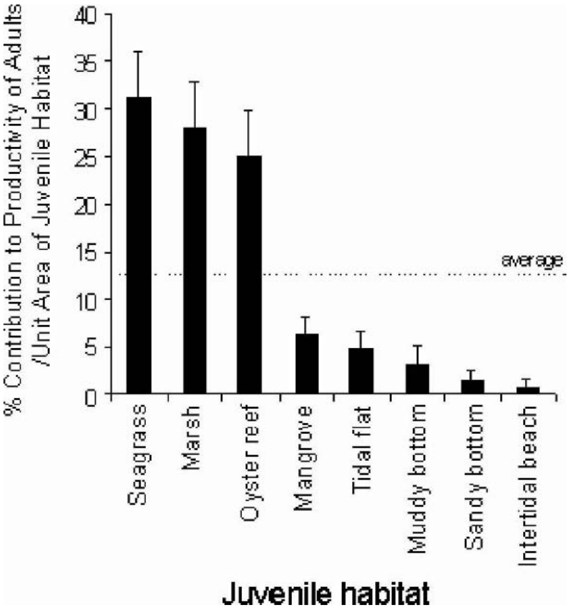

Fig. 2. An hypothetical comparison of the nursery value of several different habitats. The dashed line represents the average percentage productivity of adults per unit area from all juvenile habitats. In this example, seagrass meadows, marshes, and oyster reefs are nursery habitats (from Beck et al. (2001) published with permission. Copyright, American Institute of Biological Sciences).

South Wales, Australia) 80% of individuals and 8 of the 13 species were juveniles of species found only on coastal reefs as adults (Hair et al., 1994). Until recently, the nursery role concept had rarely been clearly stated making testing of such a concept difficult (Beck et al., 2001). It is not simply a matter of quantifying the numbers of juveniles within seagrass habitats. Rather, a definitive test requires a comparison among all habitats that juveniles use and quantification of not only density, but also growth, survival of juveniles, and movement to adult habitats (Beck et al., 2001) (Fig. 2).

Seagrass beds are important feeding habitats for juvenile and adult fishes. The major prey categories for omnivorous and carnivorous fishes from seagrass habitats are crustaceans (e.g. Heck and Weinstein, 1989; Greenway, 1995; Hindell et al., 2000b). In a dietary study of fishes from Western Port (Victoria, Australia), crustaceans were the dominant prey of the majority (69%) of the 88 species investigated (Edgar and Shaw, 1995b). Besides fish that are resident (either temporary or permanent) in seagrass beds, nocturnally active fish (e.g. Haemulidae, Lutjanidae), may migrate to seagrass beds to feed (Nagelkerken et al., 2000a). Seagrass beds also provide an important foraging habitat for a variety of mobile predatory fishes. Seven species of fishes caught over seagrass beds in Port Phillip Bay (54% of predatory species caught in the study) consumed fishes, although no species were exclusively piscivorous (Hindell et al., 2000b). The prey included seven fish families and represented 36.8% of the families occurring in seagrass (Hindell et al., 2000b) (see also VI.C, Trophic linkages).

III. Comparison of Abundance, Diversity, Growth, and Survival of Fish in Seagrass Habitats, with Other Nearshore Habitats

The relative value of seagrass compared to other habitats (e.g. marsh, mangrove, non-vegetated) has typically been estimated by comparing densities of organisms among habitats (Fig. 2). A basic assumption of such studies is that high animal densities indicate high habitat quality and preferred habitat (Rozas and Minello, 1998). Most comparisons among habitats have contrasted seagrass with nearby non-vegetated substrates, and few studies have compared the potential range of habitats available or investigated linkages between different habitats (but see Parrish, 1989; Gillanders and Kingsford, 1996). In a recent review, Heck et al. (2003) found that most results were consistent with the expectation that abundance, growth, and survival were greater in seagrass than in non-vegetated habitats. However, they found few significant differences existed in abundance, density, and survival when seagrass habitats were compared to other structured habitats (oyster and cobble reefs, macroalgal beds) and that structure per se, rather than the type of structure, may determine value of a nursery habitat.

A. Between Seagrass Species

In general, the importance of seagrass beds to numerous animals is well understood, but few studies have investigated how abundance, growth, mortality, and structure of assemblages vary among different species of seagrass. Such information is particularly important where many species of seagrass occur (e.g. tropical Australia, Loneragan et al., 1998). Several studies have found that the abundance of organisms does not differ between different seagrass species (e.g. Middleton et al., 1984; Loneragan et al., 1998; but see Rooker and Holt, 1997), although the structure of assemblages and size of organisms may vary (Middleton et al., 1984; MacArthur and Hyndes, 2001). For example, mean species richness and mean abundance of fishes did not differ between *Posidonia australis* and *Zostera capricorni* at similar depths in Botany Bay (New South Wales, Australia), but marked differences were found in the structure of the assemblages (Middleton et al., 1984). In addition, *Zostera* tended to be dominated by smaller fish species and individuals, whereas larger species and individuals were found in *Posidonia* (Middleton et al., 1984). For example, smaller species of the Gobiidae and Syngnathidae were found in *Zostera*, whereas larger members of these families were found in *Posidonia*. Juveniles of several species were thought to move from *Zostera* to *Posidonia* with increased size. In some comparisons between different species of seagrass, it is difficult to distinguish the effects of habitat structure from those of water depth (e.g. Jenkins et al., 1997b).

Mixed results were found regarding differences in growth rates of animals among seagrass species. For example, tiger prawns (*Penaeus esculentus* and *P. semisulcatus*; Penaeidae) grew significantly faster in seagrass beds where *Enhalus acoroides* dominated (Loneragan et al., 1998), whereas no significant difference in growth of red drum (*Sciaenops ocellatus*; Sciaenidae) between *Halodule wrightii* and *Thalassia testudinum* seagrass was found (Rooker and Holt, 1997). The latter authors suggested that fish may select habitats where mortality rates are lowest. Although predation between the two types of seagrass was similar, it was difficult to determine the significance of this result because shoot density and other morphological features (e.g. blade widths, blade height) also varied (Rooker et al., 1998a).

Comparisons of animal abundance also have been made between natural and artificial seagrass (e.g. Bell et al., 1985; Sogard, 1989), and between natural seagrass and transplanted beds (e.g. Sheridan et al., 2003). No significant differences in number of individuals were found between natural and artificial seagrass, but there were significantly fewer species in artificial seagrass, possibly because artificial seagrass was submerged for less time (Bell et al., 1985). Natural seagrass had significantly higher densities of fishes, decapods, annelids, and benthic crustaceans than transplanted shoalgrass (*Halodule wrightii*) and the assemblages differed (Sheridan et al., 2003; see also Section VII.C of this chapter).

B. Seagrass/Non-vegetated Habitats

The majority of comparisons have involved abundances of organisms in seagrass habitats with those in nearby non-vegetated habitats. Frequently, sampling has been restricted to one seagrass and one non-vegetated habitat at a single site or limited to one bay or estuary where more than one site was used (Ferrell and Bell, 1991). Comparisons of density between seagrass and nearby non-vegetated habitat have generally found significantly higher densities of organisms in seagrass compared to non-vegetated habitats (see Heck et al., 2003 and references therein) (but see Hanekom and Baird, 1984; Heck and Thoman, 1984; Petrik et al., 1999). In addition, the number of species is generally greater within seagrass habitats than in non-vegetated habitats (e.g. Gray et al., 1996; Jenkins et al., 1997b; Jenkins and Wheatley, 1998; but see Jordan et al., 1997). The number of species was, however, found to decrease in non-vegetated habitat with increasing distance from seagrass (Ferrell and Bell, 1991). Nagelkerken et al. (2001) also found that fish abundance and species richness were high in non-vegetated habitats near seagrass and mangroves. Enhanced diversity and abundance of prey (e.g. Lubbers et al., 1990; Connolly, 1997; Jenkins and Hamer, 2001), increased microhabitat availability, reduced risk of predation, and hydrodynamic effects on larval supply are all thought to contribute to increased animal abundance and species richness within vegetated habitats (Orth, 1992; Jordan et al., 1997) (see also 'Spatial scales—factors influencing abundance of fish in seagrass beds', Section IV).

The composition and relative abundance of mobile invertebrates and fish in seagrass and non-vegetated habitats are often distinctly different (e.g. Connolly, 1994a; Gray et al., 1996). Differences in such assemblages occur because many species consistently occur in only one habitat. Seagrass habitats tend to be dominated by small cryptic species and juveniles of larger species, whereas non-vegetated habitats tend to be dominated by species that avoid predation by schooling or employing camouflage (Jenkins et al., 1997b). Fish assemblages from seagrass habitats were more similar to those from non-vegetated habitat within 10 m of seagrass than to those greater than 100 m from seagrass (Ferrell and Bell, 1991).

Experimental evidence also suggests that individuals inhabiting seagrass experience reduced predation rates compared to organisms in non-vegetated

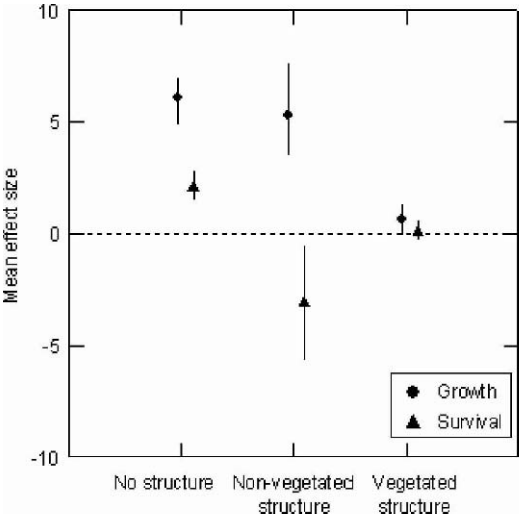

Fig. 3. Juvenile survival and growth rates in seagrass meadows (zero or dotted line) compared to no structure (e.g. sand, soft sediment, etc), non-vegetated structure (e.g. cobble, oyster reef etc.) and vegetated structure (e.g. macroalgae, salt marsh) as calculated from meta-analyses. Positive values indicate greater survival or growth of juveniles in seagrass than in alternative habitats, whereas negative values indicate lower survival or growth in seagrass. Where the confidence intervals overlap zero (dotted line) there was no significant difference between seagrass and the alternative habitat. Shown is the mean effect size calculated using bias-corrected Hedges' *d* and 95% confidence intervals (bias corrected) calculated from 5,000 bootstrap iterations of the data (see Heck et al., 2003 for further details). Sample sizes were: no structure ($n = 47$ and 8 for survival and growth comparisons respectively), non-vegetated structure ($n = 10$ and 62) and vegetated structure ($n = 12$ and 21). Data were taken from Tables 3 and 5 in Heck et al. (2003), reproduced by permission of Inter-Research.

areas (see Heck et al., 2003 and Heck and Orth, Chapter 22, for a list of references), most likely due to the structure and complexity provided by seagrass (Fig. 3). A meta-analysis of survivorship data found that survival of juvenile fish and invertebrates was significantly higher in seagrasses than unstructured habitats (Heck et al., 2003). However, Peterson et al. (2001) only found this pattern at their temperate seagrass site and not at their subtropical seagrass site, although they note that different species of seagrass were found at the two sites.

When all studies (total = 11) comparing growth rates of juvenile fish and invertebrates in seagrass were considered using a meta-analysis, growth rates were greater in seagrass habitats than in unstructured habitats (Heck et al., 2003) (Fig. 3). For invertebrates, variable responses of growth to the presence of seagrass have been found (Heck et al., 1997). Likewise, caging studies examining growth of organisms have found variable responses between seagrass and non-vegetated habitats (e.g. Sogard, 1992; Heck et al., 1997; Meng et al., 2000; Phelan et al., 2000) (but see Irlandi and Peterson, 1991; Stunz et al., 2002). Growth of fish has also been estimated using otolith microstructure. Fish collected from vegetated and non-vegetated habitats showed similar growth histories including over a 10-day period (Stunz et al., 2002). Fish may, however, have moved among habitats over this period of time. These results differed from growth rates measured from fish held in enclosures (i.e. where movement was restricted) where there was increased growth in vegetated habitats (seagrass and salt marsh) relative to non-vegetated habitats (Stunz et al., 2002).

C. Seagrass/Algae

Comparisons of density and species diversity in seagrass and algal habitats are few compared to the number of studies comparing seagrass to non-vegetated habitats (but see Sogard and Able, 1991; Haywood et al., 1995; Sheridan et al., 1997; Jenkins and Wheatley, 1998; Guidetti, 2000; Nagelkerken et al., 2000b). Fish are generally more abundant in seagrass than algal habitats, with both of these habitats having greater densities than non-vegetated habitats (Jenkins and Wheatley, 1998; Guidetti, 2000). Similar densities of crustaceans have been found in seagrass and algal habitats (e.g. Sogard and Able, 1991; Haywood et al., 1995). Assemblages of animals in seagrass and algal habitats differ, but assemblages are more similar to each other than to assemblages found over unstructured bare sand or mud (e.g. Jenkins and Wheatley, 1998; Guidetti, 2000). It was suggested that fish respond to habitat structure per se rather than to specific characteristics of the habitat (Jenkins and Wheatley, 1998).

Few studies have compared survival and growth between seagrass and algal habitats. Although settlement of Atlantic cod (*Gadus morhua*; Gadidae) was similar among four types of habitat (sand, seagrass, cobble, and rocky reef), survival differed greatly among habitat types and was correlated with habitat complexity (Tupper and Boutilier, 1995). In addition, elevated growth rates were found in seagrass habitats (Tupper and Boutilier, 1995).

D. Seagrass/Mangroves

Several studies have compared densities of fish between seagrass and mangrove habitats, although some of these have only sampled the area adjacent to the mangrove prop root habitat and have not used quantitative methods (Sheridan and Hays, 2003). Densities of juvenile fish were significantly lower in seagrass than adjacent mangrove habitats (Robertson and Duke, 1987; Laegdsgaard and Johnson, 1995; Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2002). Sheridan (1992), however, noted that the majority of species either exhibited no difference in densities or lower densities within mangrove habitats as compared to seagrass habitats. In a recent review that only used studies that utilized quantitative methods, Sheridan and Hays (2003) found that nekton densities were not consistently enhanced in mangroves relative to other habitat types including seagrass. While quantitative methods have been used to compare seagrass to mangrove habitats, most studies have used different sampling methods in each habitat. Given that different types of sampling equipment can result in differences in densities of organisms within a habitat, it is difficult to draw strong conclusions from any of the comparative studies. Distinct differences in mangrove and seagrass assemblages have also been found (Robertson and Duke, 1987; Laegdsgaard and Johnson, 1995). The presence of adjacent mangroves enhanced the abundance and species richness of fish in seagrass beds (Nagelkerken et al., 2001). However, it should be noted that mangrove habitats in some regions may only be available to fish and invertebrates at high tide and organisms must move to other habitats at low tide, thus, the overall importance of mangrove habitats may be overestimated.

Few studies have compared survival of organisms between seagrass and mangroves. Survival of tethered fish did not vary between mangrove and seagrass habitats, but was significantly less in non-vegetated habitats (Laegdsgaard and Johnson, 2001). In contrast, predation on tethered spiny lobsters was greater in seagrass than in mangrove habitats (Acosta and Butler, 1997). No comparisons have been done of growth of organisms between seagrass and mangrove habitats (Sheridan and Hays, 2003).

E. Seagrass/Marshes

In a review utilizing meta-analyses of density, growth, and survival of organisms in salt marsh, Minello et al. (2003) found that the nursery value of salt marsh habitats was less than that of seagrass habitats (Fig. 4). In their analysis of 32 studies

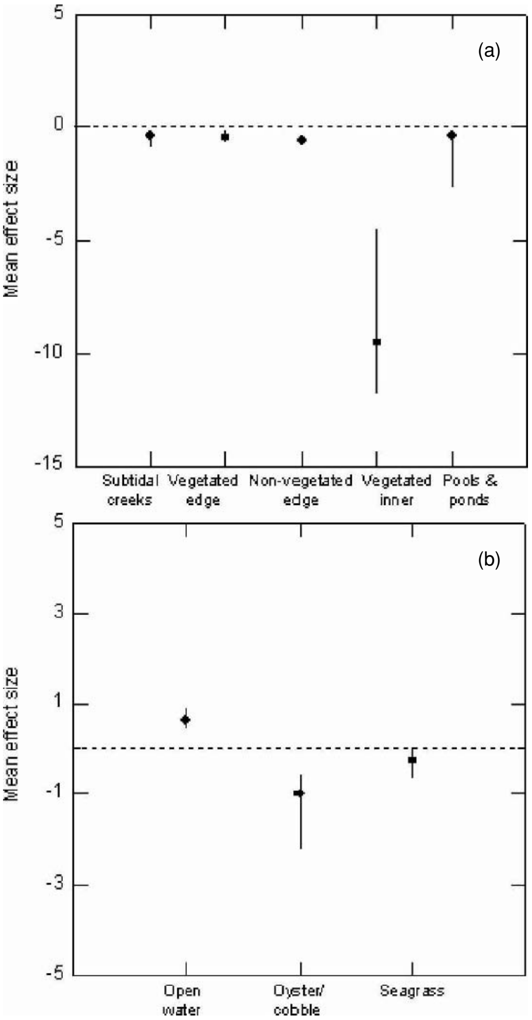

Fig. 4. (a) Density of nekton in various regions of the marsh relative to seagrass meadows and (b) survival in salt marsh relative to other types of habitat (e.g. open water, oyster/cobble, and seagrass) as calculated from meta-analyses. The experimental habitat type was marsh in (a) and (b), whereas the control habitat was the seagrass in (a) and the open water, oyster/cobble, and seagrass in (b). Positive values indicate greater density or survival in the experimental habitat type relative to the control habitat, whereas negative values indicate lower densities in the experimental habitat. Where the confidence intervals overlap zero (dotted line) there was no significant difference between the two habitats being compared. Shown is the mean effect size calculated using Hedges' *d* and 95% confidence intervals calculated from 999 bootstrap iterations of the data (see Minello et al., 2003 for further details). The number of density comparisons was 38, 17, 150, 4 and 4 for comparisons between seagrass and subtidal creeks, vegetated edge, non-vegetated edge, vegetated inner, and pools and ponds respectively. The number of survival comparisons was 30, 4, and 10 for comparisons between salt marsh and open water, oyster/cobble and seagrass respectively. Data were taken from Tables 4 and 9 in Minello et al. (2003), reproduced by permission of Inter-Research.

that compared densities of organisms, they found that seagrass habitats had higher animal densities than various regions of a marsh (e.g. vegetated marsh edge, non-vegetated marsh, vegetated inner marsh) (Minello et al., 2003 and references therein). Organisms may, however, initially settle in seagrass habitat and then move to marsh habitats or alternatively, marsh habitats may have increased rates of predation (e.g. Orth and van Montfrans, 1987).

Tidal inundation patterns may be important in determining habitat use (of both marsh and mangroves) because shoreline habitats that are not flooded cannot be used by most organisms. Rozas and Minello (1998) compared seagrass and marsh habitats where flooding durations for each habitat type were similar. They found that total number of fishes was not significantly different in salt marsh and seagrass. Many Australian marshes may only be flooded during high tides and for relatively short periods of time. Densities of fish in salt marsh in Australia are less than 1 fish per m^2, whereas in seagrass fish are at densities greater than 1 m^2 (Connolly, 1994a; Connolly et al., 1997; Thomas and Connolly, 2001). Thus, utilization of marsh habitats in Australia is significantly less than seagrass habitats. In addition, differences in submergence time between seagrass and salt marsh habitats may also occur within the USA (Rozas and Minello, 1998).

Survival of animals in seagrass does not appear to be significantly different from that in salt marsh (reviews: Heck et al., 2003; Minello et al., 2003) (Fig. 4). For example, survival time for tethered brown shrimp (*Farfantepenaeus aztecus*, Penaeidae) was similar between seagrass and marsh habitats and significantly greater than over non-vegetated sand bottom (Minello, 1993).

Very few studies have compared growth of fish or invertebrates in seagrass and marsh habitats (but see Irlandi and Crawford, 1997; Phelan et al., 2000; Stunz et al., 2002) and most of these studies differ in the species examined and methodology utilized. Minello et al. (2003) combined all studies in a meta-analysis and found that growth in seagrass was significantly greater than growth in non-vegetated marsh (sensu Minello et al., 2003). However, their meta-analyses also found that growth in vegetated marsh was significantly higher than in non-vegetated marsh. Stunz et al. (2002) using solid-walled field mesocosms found no significant difference in growth of *Sciaenops ocellatus* (Sciaenidae) between the edge of vegetated marsh and seagrass. Irlandi and Crawford (1997) used field enclosures containing vegetated marsh edge with seagrass and vegetated marsh edge without seagrass to evaluate growth of *Lagodon rhomboides* (Sparidae). They found that growth was negative (measured as biomass) in vegetated marsh without seagrass and positive in vegetated marsh with seagrass. Thus, seagrass appears to have an effect on growth of this species of fish.

IV. Spatial Scales—Factors Influencing Abundance of Fish in Seagrass Beds

Seagrass habitats represent a series of hierarchical scales ranging from single blades to individual short shoots to groups of short shoots composing a seagrass bed to the seagrass bed within a matrix of other habitat types (e.g. non-vegetated habitats) to submerged vegetation within the large coastal system (Robbins and Bell, 1994). The scale at which observations are made or experiments are conducted may influence results and conclusions (Turner, 1989), such that patterns and processes that are found to be important at one scale may not be important at another scale (Wiens, 1989).

A large amount of research has focused at the small scale (e.g. seagrass blade length and density) and shown that this scale is important in influencing recruitment dynamics (see below and Heck and Orth, Chapter 22). Artificial seagrass has been used in many of the small-scale experiments addressing a variety of questions, as it provides a standard habitat unit where morphological aspects of the plants can either be held constant across a number of locations or manipulated such that spatial variation is not a confounding influence. Research at this small scale has been reviewed elsewhere (e.g. Bell and Pollard, 1989) and is only briefly mentioned here. The focus on larger-scale spatial patterns and linking seagrass patch size, shape, or complexity of patch perimeter, position of a patch in the seagrass bed or its position in relation to adjacent patches and other habitats, to the structure and function of assemblages has only recently been investigated. At this larger spatial scale, a range of scales (extent, sensu Wiens, 1989) and sampling units that vary in scale (grain, sensu Wiens, 1989) have been used making comparisons among studies difficult.

Table 1. Summary of factors influencing abundance, growth, survival, and movement of organisms at different spatial scales.

Spatial scale	Distances	Variable	References
Within patches	cm to m	Shoot density, shoot length and width, above/below-ground biomass	Bell and Westoby (1986a,b,c); Bell et al. (1987); Steffe et al. (1989); Worthington et al. (1991, 1992)
Among patches	m to 10s of m	Patch size	McNeill and Fairweather (1993); Irlandi (1997); Eggleston et al. (1998a, 1999); Irlandi et al. (1999); Hovel and Lipcius (2001)
		Patch shape	Tanner (2003)
		Orientation of patches	Tanner (2003)
		Percent cover of seagrass	
		Edge vs. center	Bologna and Heck (1999, 2000); Bell et al. (2001); Peterson et al. (2001)
Landscape scale	10s of m to km	Degree of heterogeneity or patchiness	Irlandi et al. (1995); Salita et al. (2003)
		Patch isolation	Turner et al. (1999); Hovel and Lipcius (2002)
		Position of patches within landscape	Bell et al. (1988); Sogard et al. (1989b); Jenkins et al. (1996); Hannan and Williams (1998)
		Adjacent habitats	Irlandi and Crawford (1997); Eggleston et al. (1999); Nagelkerken et al. (2001); Nagelkerken and van der Velde (2002)
Regional and biogeographic scales	10s to 100s km and greater	Among estuaries	Worthington et al. (1992); Ferrell et al. (1993); Wyda et al. (2002)
		Among biogeographic regions	Heck et al. (2003)
		Tropical vs. temperate systems	Weinstein and Heck (1979); Heck and Wilson (1987); Costa et al. (2002)

A. Patch Scale Variables

1. Within Patches

Structural components of seagrass beds occurring at the scale of tens of centimeters to meters (e.g. shoot density, blade length and width, and above- and below-ground biomass) may influence abundance, growth, and survival of organisms (Table 1). Seagrass structure may enhance density of fish through a reduction in predation risk (reduced predation rates or reduced efficiency of predators) as demonstrated by experimental studies. Increased structural complexity (e.g. shoot density, blade width) of habitats has, for example, been shown to reduce predation rates (e.g. Heck and Thoman, 1981; Orth et al., 1984; Minello, 1993; Rooker et al., 1998a; Peterson et al., 2001; Stunz and Minello, 2001; Orth and van Montfrans, 2002) (see also Heck and Orth, Chapter 22).

Where predation rates are low, survival rates should be high which could lead to an increase in abundance. However, abundance of fish also may be increased in dense seagrass relative to sparse seagrass because food availability is greater within dense seagrass (e.g. Bell and Westoby, 1986b). Fish abundance generally increases with seagrass density (e.g. Bell and Westoby, 1986a,b,c; Steffe et al., 1989; Worthington et al., 1992), although Bell and Westoby (1986b) noted that such a relationship was only found for individual species (e.g. *Stigmatopora argus*, *Bathygobius kreffti*, *Alpheus* sp.) and not for groups of species or other assemblage measures (e.g. total abundance). A lack of relationship at the assemblage level was largely due to different species showing different responses. Four of the six species that were common in both *Zostera capricorni* and *Posidonia australis* showed a similar response in the two seagrasses (Bell and Westoby, 1986b). The relationship between abundance of fish and density of seagrass shows an asymptotic response. For example, the abundance of fish increased greatly between 0 and 25 seagrass blades per m^2, but abundances of fish were similar when density of seagrass was between 25 and 400 blades per m^2 (Worthington et al., 1991).

Although abundances of fish and invertebrates within single beds of seagrass (e.g. plots of 25 m^2) showed noticeable effects when leaf height and density were manipulated, correlations between abundances of organisms and complexity of seagrass at the larger spatial scale were rare (Bell and Westoby, 1986c). Environmental features (e.g. distance from ocean, grain size of sediment, area of seagrass bed) also failed to account for differences in abundances and Bell and Westoby (1986c) concluded that stochastic settlement from the plankton may cause variation in density of organisms. A model of hierarchical habitat selection, in which juveniles select the first seagrass bed they encounter and then after settlement select microhabitats within the seagrass bed that provide food and a high level of protection from predation, was proposed to explain the distribution of fish in seagrass beds (Bell and Westoby, 1986a; Bell et al., 1987). Settlers of blue groper (*Achoerodus viridis*, Labridae) did not discriminate between artificial seagrass units (ASUs) with dense and sparse covers of leaves, which supports the above model (Bell et al., 1987). This 'settle and stay' hypothesis was not supported by other studies in which the turnover rate appeared to be high (Jenkins and Sutherland, 1997). Although the study of Jenkins and Sutherland (1997) did not distinguish between movement and mortality, the appearance of post-settlement juveniles within 24 h of clearances suggests rapid migration to seagrass. Thus, correlations between physical complexity of seagrass and abundances of fish and invertebrates would be unlikely at broad spatial scales, but if individuals move around within seagrass beds to select habitats (e.g. density and height of seagrass) that favor survival, then correlations would be common at the small spatial scale (Bell and Westoby, 1986c).

2. Among Patches

Although abundances of fish and invertebrates are often correlated with seagrass structure (e.g. biomass, shoot density, shoot length) within seagrass beds, these correlations tend to break down at larger spatial scales. At the individual patch level (i.e. contiguous area of seagrass habitat that differs in appearance from surrounding habitat), which generally covers scales of meters to tens of meters, the size, shape, and orientation of patches, as well as percent cover of seagrass has been shown to influence not only the abundance and species composition of organisms within patches, but also rates of predation on patch inhabitants, and growth (Table 1). Most of this research has focused on the effect of habitat fragmentation (e.g. edge vs. center of habitats; patch size) and on responses by invertebrates. The individual habitat patch also may be considered in a landscape mosaic (see 'Landscape scale variables', Section IV.B, and Bell et al., Chapter 26).

Habitat destruction resulting in habitat loss per se and habitat fragmentation (which creates a greater number of habitat patches that are smaller in size than the original contiguous tract of habitat, Bender et al., 1998) may influence abundance of species. Although the effect of habitat loss is obvious in that when habitat is removed, species within them are subsequently displaced and may also be lost, the effects of habitat fragmentation are less obvious (Bender et al., 1998). Habitat fragmentation may differentially affect the abundance of species depending on whether individual species preferentially utilize interior sections of habitat, areas along edges of patches, or show no preference. One would expect that as habitats are fragmented, interior species would decrease in abundance, edge species would increase in abundance, and generalist species that show no preference for either the edge or the interior of habitats would show no difference in abundance (Bender et al., 1998). Bell et al. (2001) found little evidence identifying any taxonomic group to be edge sensitive, although infaunal bivalves appeared to act as interior species in the majority of studies surveyed. Thus, infaunal bivalves would be expected to show a disproportionate decrease in abundance as patch size decreased due to the increase in edge habitat relative to interior habitat (Bell et al., 2001).

Higher densities of bivalves (including bay scallops) have been found at edges of seagrass beds than in the interior or in nearby non-vegetated sediments (Bologna and Heck, 1999, 2000). Since predation rates were increased along edges of *Thalassia testudinum* beds relative to the other habitats, and growth rates also were significantly higher, individual scallops appeared to trade off an increased predation rate for increased growth rates (Bologna and Heck, 1999). No significant difference in predation pressure between edge and center of *Zostera marina* habitats was found, although these habitats had significantly less predation than non-vegetated habitats (Peterson et al., 2001).

As habitats are fragmented, patches of different sizes may be found. It is predicted that more individuals may be found (per unit area) as patch size decreases (Bell et al., 2001). Naturally occurring beds of *Zostera capricorni* and *Posidonia australis* supported significantly more species of fish and macroinvertebrates in two small beds than in one large bed of the same total area (McNeill and Fairweather, 1993). Despite these correlative results, ASUs showed few significant differences between two small (7 m^2) ASUs and one large (14 m^2) ASU in experimental manipulations (McNeill and Fairweather, 1993). In another experimental study, only two of the seven response variables (namely, grass shrimp and small, mobile crustaceans) showed increased density in small patches relative to large patches (Eggleston et al., 1999). These two species may be responding to an edge effect since they were two times more likely to encounter a small patch (0.25 m^2) than a large (1 m^2) patch (Eggleston et al., 1999). However, another study involving both a literature review and a survey of fish and epibenthic amphipods in Tampa Bay, Florida, reported that patch size had no consistent effect on resident fauna over spatial scales from <1 to $>5{,}000$ m^2 (Bell et al., 2001). An organism's response to habitats of different patch sizes may also be species-specific (Eggleston et al., 1998a). In terrestrial studies, the degree of isolation and position of patches within the landscape is important and may account for differences between marine studies (Bell et al., 2001) (see also 'Landscape scale variables', Section IV.B).

Survival of organisms may also be related to patch size in that small patches have greater edge to area ratios than large patches, theoretically leading to increased predation in small patches since prey should be more available to predators. However, an inverse relationship was found between crab (*Callinectes sapidus*, Portunidae) survival and patch size, highlighting the need for empirical research on fragmentation effects (Hovel and Lipcius, 2001). Hard clams (*Mercenaria mercenaria*, Veneridae) showed increased survival in large rather than small seagrass patches and in continuous vs. patchy seagrass, but seagrass complexity (e.g. shoot density, root biomass) also differed among treatments making interpretation of the significance of these results difficult (Irlandi, 1994, 1997). To date, only one study (that of Hovel and Lipcius, 2001) has demonstrated a negative correlation between prey survival and patch size in marine systems. This study is the only one that has used a range of levels of fragmentation of natural seagrass (e.g. patches <1 to $>30{,}000$ m^2) and tested how these levels of fragmentation influence faunal survival without seagrass complexity varying among different levels of fragmentation.

Growth of clams was increased in the center of large seagrass beds compared to small seagrass beds, although there was no increased abundance of organisms in the center of large beds (Irlandi, 1997). Growth of bay scallops (*Argopecten irradians concentricus*, Pectinidae) was slightly faster in naturally occurring small patches of seagrass than in large patches, although the difference was not thought to be biologically meaningful (Irlandi et al., 1999). Patch size did not, however, influence overall predation rates on juvenile scallops (Irlandi et al., 1999).

Patch shape and orientation also may influence abundance of organisms, but there have been few empirical studies. In one such study, fish showed decreased abundance in elongate patches perpendicular to the prevailing current compared to square patches or elongate patches parallel to the prevailing current (Tanner, 2003). This orientation effect was related to movements between intertidal areas and subtidal refuges (Tanner, 2003). Although individual patch characteristics have been shown to be important, the landscape context also needs to be considered and may account for variation among studies.

B. Landscape Scale Variables

1. General

Very few studies of marine systems have employed a landscape perspective (but see Bell et al., 1988; Bell and Hicks, 1991; Irlandi et al., 1995; Irlandi and Crawford, 1997; and Bell et al., Chapter 26). Most studies within a landscape perspective have focused on either proximity to other habitats (e.g. adjacent habitats) or on the position of seagrass beds within a bay or estuary (e.g. position of patches within a landscape). Further research is clearly needed on landscape scale variables that operate at the scale of tens of meters to kilometers (Table 1).

2. Degree of Heterogeneity or Patchiness

Few studies have investigated how the degree of heterogeneity of seagrass may influence abundance, growth, or survival of fish and invertebrates. The abundance of fish was influenced only by continuity of vegetation and not by morphology, suggesting that continuous uninterrupted beds should be preferred to patchy beds due to greater protection from predators (Salita et al., 2003). Rates of predation on bay scallops (*Argopecten irradians*, Pectinidae) were similar among very patchy, patchy, and continuous seagrass habitat in short-term experiments (24 h), but more scallops were taken from very patchy seagrass beds over longer time periods (Irlandi et al., 1995). Increased predation in seagrass patches may occur because non-vegetated habitats that surround patches allow access to predators. Further studies are needed to test the generality of these patterns.

3. Patch Isolation

Although habitat fragmentation may create a greater number of habitat patches that are smaller in size than the original contiguous tract of habitat, it may also result in spatially isolated remnant patches. The isolation of patches may affect hydrodynamic conditions with associated affects on benthic assemblages (Turner et al., 1999). The effect of patch isolation on abundance, growth, and survival of organisms in seagrass systems remains largely unexplored (but see Hovel and Lipcius, 2002). Crab (*Callinectes sapidus*, Portunidae) survival was higher in connected patches than where seagrass patches were isolated, but was not correlated with patch size or seagrass structural complexity, suggesting that the non-vegetated sediment surrounding patches may have acted as a corridor allowing predators access to seagrass patches (Hovel and Lipcius, 2002). Further empirical research using both fish and invertebrates is needed to determine how isolation may affect abundance, growth, and survival of organisms. In addition, patch isolation may be particularly important in determining whether organisms can successfully move among patches and to adult habitats.

4. Position of Patches Within Landscape

The species composition and abundance of fish and invertebrates can vary considerably among seagrass beds within an estuary (Bell et al., 1988; Sogard et al., 1989b; Jenkins et al., 1996; Hannan and Williams, 1998). Frequently, one site within an estuary was found to have consistently high or low abundances of one or two species through time despite sites being chosen to minimize differences (Ferrell et al., 1993). For example, a single site in Botany Bay (NSW, Australia) had consistently high recruitment among a range of species compared to other sites within Botany Bay and elsewhere (McNeill et al., 1992).

The distance to the mouth of the estuary may affect the distribution and abundance of fish and invertebrates in seagrass beds because larvae of different species are often found in different parts of an estuary and the structure (height and density of seagrass leaves), size, and shape of seagrass beds often varies throughout the estuary (Bell et al., 1988). Because the structure of seagrass beds may vary throughout the estuary, differences in vegetational characteristics also may contribute to differences in abundances (e.g. Sogard et al., 1989a). In addition, water circulation patterns and physical factors (e.g. temperature and salinity) are likely to vary at this broader spatial scale. Species richness and abundances of common species varied among zones along an estuary and among arms of the estuary, but these differences were not due to physical complexity of seagrass or to temperature and salinity gradients (Bell et al., 1988). Differences among zones of the estuary were attributed to the combined effects of spawning location and nature of eggs and larvae; species that spawned within the estuary and had demersal eggs were most abundant furthest up the estuary, whereas those that spawned at sea or near the mouth of the estuary and had pelagic eggs were found closest to the mouth of the estuary (e.g. Bell et al., 1988; Hannan and Williams, 1998). No studies have investigated whether growth or survival of organisms may also vary along this scale.

A conceptual model of factors that have the potential to influence assemblages and densities of fishes in seagrass beds in Florida Bay was proposed by Sogard et al. (1989a) (Fig. 5). The model suggests that initial densities of juveniles depend on recruitment from the larval pool, which is dependent on the intensity of adult reproduction and passive immigration from other areas. Survival of larvae is constrained by both physical and biological interactions. Larval duration, regional hydrodynamics, and larval behavior also may influence recruitment patterns (Jenkins et al., 1998). Once recruited, juveniles and adults

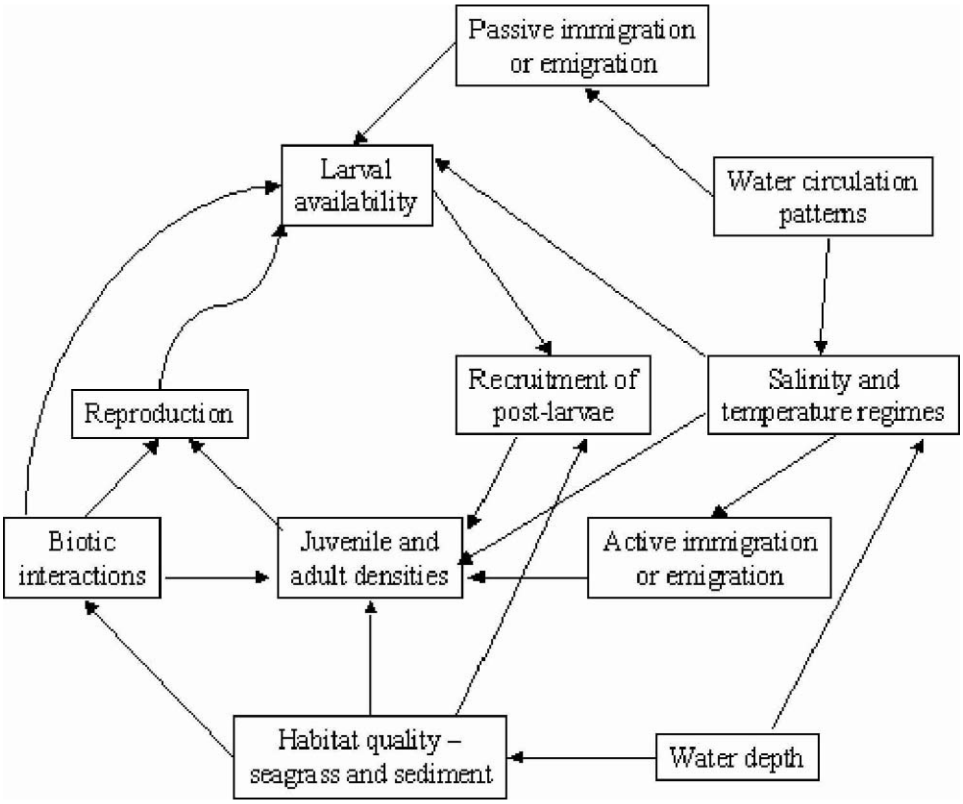

Fig. 5. A conceptual model of potential factors influencing species composition and densities of fishes residing in seagrass habitats. From Sogard et al. (1989a). Reproduced by permission of Bulletin of Marine Science.

may redistribute themselves depending on behavioral selection of preferred habitats and physical extremes (e.g. Jenkins et al., 1996). Physical transport patterns also may influence distribution of presettlement larvae, whereas physical disturbance (e.g. wave action) may influence post-settlement losses (Jenkins et al., 1997a). Biotic interactions, which may be influenced by characteristics of the seagrass canopy, may also be important once organisms have recruited.

5. Adjacent Habitats

Relatively little information exists on how linkages among habitats may affect the structure and dynamics of marine assemblages (but see Robbins and Bell, 1994; Irlandi and Crawford, 1997) compared to terrestrial systems (Micheli and Peterson, 1999). Never the less, it is clear that adjacent habitats may have significant effects on both abundance and diversity of organisms, on predator–prey interactions, and on movements of organisms between habitats (see Bell et al. Chapter 26).

In a comparison of bays with and without seagrass beds (and/or mangroves), juveniles of 17 fish species were abundant in seagrass dominated bays, but these species were largely absent in bays lacking seagrass (Nagelkerken et al., 2001). In a subsequent study, Nagelkerken et al. (2002) found that 11 of these 17 species were completely absent or occurred in low densities as adults on islands lacking seagrass, and they concluded that the presence and abundance of several fish species on coral reefs are a function of adjacent habitats, namely the presence of nearby bays containing seagrass (and/or mangroves).

Species richness may be increased when other types of habitats are present. However, in an experimental study, in which colonization to artificial seagrass, oyster shell, and mixed habitats was investigated, the total species number and density of macrofauna was not higher in the mixed habitat treatment compared to the seagrass or oyster shell treatments (Eggleston et al., 1999). Similar species occurred in seagrass and oyster shell habitats, such that there was no additive effect on overall species richness (Eggleston et al., 1999).

The abundance and growth of pinfish (*Lagodon rhomboides*, Sparidae) were greater where intertidal salt marsh was adjacent to seagrass beds rather than non-vegetated habitats (Irlandi and Crawford, 1997). Movement of fish also was affected by the type of subtidal habitat adjacent to the marsh. For example, fish moved between marsh and seagrass more readily than they did between marsh and mudflat (Irlandi and Crawford, 1997). Linkages between habitats may, however, depend on the distance between habitats. These results suggest that for restoration of marsh habitats, managers may want to restore marsh habitats that are adjacent to subtidal seagrass beds (Irlandi and Crawford, 1997).

C. Regional and Biogeographic Scales

Investigations over large spatial scales (tens to hundreds of km and greater) also show significant differences in fish abundance (Ferrell and Bell, 1991; Gray et al., 1996; Goldberg et al., 2002). Observations among multiple estuaries, between tropical and temperate systems, and among different biogeographic regions may be necessary to determine if there are distinct patterns of habitat use at these large spatial scales. The generality of any observed patterns and mechanisms responsible for patterns could then be determined (Table 1).

1. Comparisons Among Estuaries

Significant variation in abundances and species richness among estuaries has been found (Worthington et al., 1992; Ferrell et al., 1993; Wyda et al., 2002). In one study that sampled three estuaries spanning 300 km of coastline, each estuary had 14 or 15 species that occurred only in that estuary (Ferrell et al., 1993). In contrast, 37 species occurred in all estuaries. Assemblages of fish from within an estuary were, however, more similar to each other than to samples from different estuaries (Ferrell et al., 1993). At large spatial scales (e.g. among 3–4 sites separated by greater than 1 km within 3–4 estuaries spanning 400 km of coast), most variation in abundances of individual species was explained by larval supply rather than density of seagrass shoots, as variation in density of shoots explained less than 5% of the variation in abundances (Worthington et al., 1992). Other factors (e.g. wave exposure) may also be correlated with larval supply meaning that determining factors that influence abundance of organisms will be difficult. In addition, attributes of seagrass structure other than density may be more important. Studies often focus on only one estuary (or location) and further research is needed to determine the generality of results among multiple estuaries.

2. Generality Across Large Biogeographic Scales

In a recent review, geographical differences were noted in the degree to which seagrass meadows support greater densities of organisms than other habitats (Heck et al., 2003). For example, 75% (58 of 77 comparisons) of studies in the northern hemisphere showed greater abundances in seagrass, whereas only 36% (42 of 116) from the southern hemisphere did. It should, however, be noted that most studies from the northern hemisphere were conducted in USA, and most studies from the southern hemisphere were conducted in Australia. Determining generality at large biogeographic scales is likely to be difficult due to differences in sampling designs and methodologies across studies and the lack of studies in some regions. Approaches using published studies and meta-analyses would be useful where studies exist for a wide range of regions, but other initiatives will be needed where existing studies are lacking. For example, a comparative study using similar techniques could be planned that enlists researchers from several countries.

3. Comparisons Between Tropical and Temperate Seagrass Systems

Relatively few studies have compared fish assemblages between tropical and temperate seagrass beds, and most of these studies only compare one tropical region to one temperate region. Frequently, numerous variables in a study differ between temperate and tropical systems (e.g. species of seagrass, patch scale variables). Therefore, determining whether latitude or some other variable is more important is difficult. Panamanian seagrass beds had significantly more species than similar habitats in the Gulf of

Table 2. Summary of factors influencing abundance, growth, survival, and movement of organisms at different temporal scales.

Temporal scale	Variable	References
Daily	Diel	Weinstein and Heck (1979); Robblee and Zieman (1984); Sogard et al. (1987); Olney and Boehlert (1988); Lubbers et al. (1990); Sogard and Able (1994); Griffiths (2001a)
	Tidal	Robertson (1980); Sogard et al. (1989c); Ryer et al. (1997); Peterson et al. (2001)
Intra-annual (seasonal)	Environmental variables	Hannan and Williams (1998)
	Characteristics of seagrass	Ferrell et al. (1993)
	Recruitment of juveniles and/or movement of larger individuals	Gillanders (1997); Rooker et al. (1998b); Griffiths (2001b)
	Larval delivery	Jenkins and Black (1994); Hamer and Jenkins (1996)
Inter-annual	Recruitment success	Jackson and Jones (1999)
	Weather patterns	Jenkins et al. (1997a)
	Habitat changes (e.g. loss and recovery)	Rasmussen (1977); Hughes et al. (2002)

Mexico, possibly due to the influence of nearby coral reefs in Panama (Weinstein and Heck, 1979). In another study, a temperate estuary (Mira estuary, Portugal) had more species (47) than a tropical estuary (Mussolo Lagoon, Angola); Syngnathidae, Gobiidae, Sparidae, and Labridae dominated the temperate estuary, whereas Haemulidae and Mugilidae dominated the tropical estuary (Costa et al., 2002). These differences were thought to reflect biogeographic patterns rather than differences in habitat types of seagrass (Costa et al., 2002).

Predation rates have also been found to vary by latitude. Increasing rates of predation among brachyuran crabs tethered in vegetated substrates were found with decreasing latitude possibly due to a greater diversity of predators at low latitudes (Heck and Wilson, 1987). Discerning latitudinal patterns will be difficult as many factors may vary between sites, only one of which is latitude.

V. Temporal Scales—Factors Influencing Abundance of Fish in Seagrass Beds

The majority of studies investigating temporal patterns in seagrass beds have focused at the small scale (e.g. diel, tidal, and seasonal patterns), and few studies have investigated differences in abundance and assemblage structure over large temporal scales (Table 2). As expected, variation in abundances of organisms was found across the range of temporal scales, although several researchers noted that spatial differences were greater than small-scale temporal differences.

A. Diel Differences

Abundance of fish in seagrass beds is often greater at night than during the day (e.g. Weinstein and Heck, 1979; Robblee and Zieman, 1984; Olney and Boehlert, 1988; Lubbers et al., 1990; Sogard and Able, 1994). However, several studies have found no diel differences in abundance of fishes (e.g. Sogard et al., 1987), and at least one study found a reduction in abundance of fish at night (Nagelkerken et al., 2000a). Such contradictory results have been found among estuaries in relatively close proximity (Griffiths, 2001a). Increased night catches may be due to increased capture efficiency caused by decreased net avoidance, movement into seagrass beds by larger more mobile fish from other habitats, and increased activity of fish as they move into the water column (Sogard et al., 1987). Despite possible diel variation, most studies report data only during the day.

Assemblages of fishes showed greater differences among estuaries than between day and night samples, suggesting that spatial variability may be greater than short-term temporal variability (Gray et al., 1998; Griffiths, 2001a). Lack of diel differences may indicate that species found in other habitats are not moving over seagrass at night or vice versa (Gray et al., 1998). However, in another study only 42% ($n = 57$) of species collected were captured during both the day and night, with 25% of species being nocturnal visitors only (Robblee and Zieman, 1984). The remaining 33% of species were collected only rarely (10 day, 9 night) (Robblee and Zieman, 1984). These differences may reflect latitudinal variation where coral reef fish frequently move over seagrass beds at night to feed, when reefs are near seagrass beds.

B. Tidal Differences

Some species may move into seagrass with the flood tide (Robertson, 1980), and other species are likely to move away from seagrass beds, particularly at extremely low tides when stranding may be a problem (Sogard et al., 1989c). Predators are expected to move into seagrass habitats with the rising tide. Therefore, predation rates should be higher at high tide than low tide, although this may be dependent on the tidal range. No significant differences in predation rates were found between tides (low vs. high) at a temperate and a subtropical site (Peterson et al., 2001). However, survival of soft crabs was greater during low tide than high tide, and this result was possibly caused by increased encounter rates between predatory crabs and molting individuals at high tide (Ryer et al., 1997).

C. Intra-annual Variability

Many studies have found seasonal differences in assemblage structure (e.g. Connolly, 1994a) and have often related these differences to environmental variables (e.g. temperature, salinity) or to characteristics of the seagrass (e.g. changes in shoot density). Frequently, differences will reflect recruitment of juveniles at several times of the year and subsequent movement of larger individuals to adjacent habitats (see also "Temporary residents of seagrass beds", Section II.C). Temporal variation in recruitment may also be influenced by coastal hydrodynamic processes which alter the delivery of larvae (Jenkins and Black, 1994; Hamer and Jenkins, 1996).

D. Inter-annual Variability

Most studies are conducted on time scales of only 1–2 years at most, making them more amenable to seasonal comparisons than to comparisons among years. Few studies have focused on time scales greater than 5 years, and most of these have considered estuaries as a whole rather than assemblages within seagrass habitats. An exception was Jackson and Jones (1999) who sampled some sites that supported seagrass over a 10-year period. They found significant annual variation in structure of assemblages and attributed this variation to differences in recruitment success. Changes in weather patterns among years (e.g. El Nino southern oscillation) may cause inter-annual variation in magnitude, timing, and number of recruitment events (Jenkins et al., 1997a). A few long-term studies have also followed the decline, loss, and recovery of seagrass and associated fish assemblages (e.g. Anderson, 1989; Hughes et al., 2002) (see also "Fate of fisheries when seagrass habitat has been lost", next and "Correlation between seagrass cover and fisheries catch", Section VI.C).

VI. Links Between Seagrass and Fisheries

A. Fate of Fisheries When Seagrass Habitats Have Been Lost

Loss or changes in species composition of seagrass may affect abundance and diversity of fish within seagrass beds, and the habitat to which juvenile fish from seagrass beds may move as adults. Numerous examples exist of widespread loss of seagrass beds (Table 3). For example, more than 4,000 ha of seagrass beds in Florida Bay were completely lost between 1987 and 1991, and an additional 23,000 ha were affected to a lesser degree (Robblee et al., 1991). Likewise, in the Galveston Bay system of Texas, 80% of submerged aquatic vegetation (SAV) has been lost since the 1970s (Pulich and White, 1991). Little information is available on how seagrass losses affect fisheries resources, and most of it is anecdotal. For example, although there were severe declines in soft shell and razor clams, lobsters, and mud crabs following the decline of seagrass at Cape Ann (Massachusetts, USA) in the 1930s, declines in fisheries of the North Atlantic were not as drastic as predicted (Thayer and Phillips, 1977). Sheridan et al. (1997) also noted that despite widespread mortality of turtlegrass (*Thalassia testudinum*) in Florida Bay and recolonization of mud patches by various algal species and shoal grass (*Halodule wrightii*), fisheries did not seem to have been affected as no long-term declines occurred in landings of important fishery organisms. However, in Western Port Bay, Australia, a decline of 70% of the seagrass cover was paralleled by a decline of about 40% in commercial fish catches (Jenkins et al., 1993). Although the results are suggestive of a link with seagrass decline, alternative explanations such as overfishing, changes in fishing effort, or larval input cannot be rejected (Jenkins et al., 1993).

Table 3. Summary of studies showing loss of seagrass and potential links to fisheries.

Location	Seagrass species	Extent of loss	New habitat type	Fishery link	Reference
European and North American coasts	*Zostera marina*	Mass destruction of *Zostera* in the 1930s	Replaced in part by other species of *Zostera*; also in some areas sediment eroded to stone reef and algal assemblages predominantly *Fucus* species	No catastrophic effect on fisheries	Rasmussen (1977)
Chesapeake Bay, east coast, USA	*Zostera marina* (major species)	Significant reduction in all species of seagrass in all sections of the bay during the 1960s and 1970s	Sparse beds of seagrass or complete lack of vegetation	Implications for commercially important species (e.g. blue crab, *Callinectes sapidus*) were thought to be considerable, but little evidence that landings declined substantially	Orth and Moore (1983); Lipcius and van Engel (1990)
Galveston Bay, Texas, USA	*Halodule wrightii* (predominantly)	Seagrass declined from 458 ha in 1956 to 0 ha by 1987	–	Shallow water habitats support commercial finfish and shellfish populations	Pulich and White (1991); Hammerstrom et al. (1998)
Western Florida Bay, Florida, USA	*Thalassia testudinum*	More than 4,000 ha of seagrass completely lost between 1987 and 1991 with an additional 23,000 ha affected to a lesser extent (>16% of total seagrass habitat)	Mud, algae and *Halodule wrightii*	Fisheries seem not to have been affected; pink shrimp, *Farfantepenaeus duorarum* yields (CPUE) did decrease following seagrass decline but increase in landings did not coincide with seagrass recovery; declines in seagrass-canopy dwelling fishes and decapod crustaceans and increases in benthic forms	Robblee et al. (1991); Thayer et al. (1994); Sheridan (1997); Sheridan et al. (1997); Matheson et al. (1999)
Botany Bay, NSW, Australia	*Posidonia australis*	Between 1942 and 1984 58% of *Posidonia* lost from southern foreshores	*Zostera capricorni* colonized many sites previously vegetated with *Posidonia*	Juveniles of commercially important species found in *Posidonia*	Middleton et al. (1984); Larkum and West (1990)
Western Port Bay, Victoria, Australia	*Heterozostera tasmanica* (predominantly)	Decline of over 70% of seagrass cover between 1973 and 1984	–	Decline of about 40% in total commercial fish catches; catches of species associated with seagrass or macroalgae declined (e.g. King George whiting, *Sillaginodes punctata*, rock flathead, *Platycephalus laevigatus*, calamari, *Sepioteuthis*	MacDonald (1992); Jenkins et al. (1993); Edgar and Shaw (1995a)

				australis, grass whiting, *Haletta semifasciata* and several leather-jacket species)	
Gippsland Lakes, Victoria, Australia	Species of *Zostera*, *Ruppia* and *Lepilaena*	Large losses of seagrass habitat in late 1910s and subsequent recovery in early 1960s	–	Decline and subsequent recovery of black bream, *Acanthopagrus butcheri* and luderick, *Girella tricuspidata*–juvenile phases associated with seagrass	MacDonald (1992)
Port Phillip Bay, Victoria, Australia	*Heterozostera tasmanica* (predominantly)	Large losses of seagrass in some areas (e.g. Geelong Arm) in early 1970s and a further decline in 1985	Soft sediment habitats may have increased as seagrass decreased	Commercial and recreational fishing important in bay; declines in species associated with seagrass (e.g. cobbler, *Gymnapistes marmoratus*, greenback flounder, *Rhombosolea tapirina*, King George Whiting, *Sillaginodes punctatus*, rock ling, *Genypterus tigerinus* and long-finned pike, *Dinolestes lewini*	Hobday et al. (1999)
Northern Spencer Gulf, SA, Australia	Intertidal (e.g. *Zostera muelleri*, *Z. mucronata*, *Heterozostera tasmanica, Posidonia australis, Lepilaena* sp. and *Ruppia* sp.) and shallow subtidal (e.g. *Amphibolis antarctica, Posidonia australis,* and *Heterozostera tasmanica*) species	Complete or partial loss of 12,717 ha of intertidal and shallow subtidal seagrasses occurring toward end of summer 1993; represents 60% of seagrass present in 1987	Both species of *Zostera* have started to recolonize intertidal areas and colonize patches within areas toward end of summer 1993; represents 60% of seagrass present in 1987	Significant area for inshore commercial and recreational fisheries formerly dominated by *Amphibolis antarctica*	Seddon et al. (2000)
Cockburn Sound, WA, Australia	*Posidonia sinuosa* but 10 sp present	From 1954 to 1978 seagrass reduced by 79%; since 1967 there has been a 77% decline	Algae form a temporary cover then bare sand	Commercially important fish and invertebrates found in seagrass	Cambridge and McComb (1984); Kendrick et al. (2002)

Alternative methods have been used to examine the effects of seagrass loss on fisheries. Three areas with seagrass beds growing immediately offshore were compared with three other areas where seagrass was lost by the early 1970s, but few clear patterns in numbers of species, numbers of individuals, and biomasses could be related to the presence or absence of seagrass (Vanderklift and Jacoby, 2003). However, it should be noted that areas with and without seagrass were not interspersed in the above study, thus spatial factors other than the presence or absence of seagrass may have led to the observed patterns. These results contrast with those of Wyda et al. (2002) who found that numbers of species, and biomass declined in areas that were degraded and where seagrass was previously present. In addition, the relative species composition altered with loss of SAV leading to higher proportions of pelagic species. The effects of loss seagrass habitat on fish assemblages have also been investigated by determining temporal patterns (decadal) of change in fish assemblages associated with the decline, loss, and recovery of seagrass (Hughes et al., 2002). Only by investigating patterns over the longer-term (decadal) were links between habitat loss and fish assemblages clearly demonstrated (Hughes et al., 2002) (Fig. 6). Long-term studies are necessary as there can be considerable site-to-site and yearly variability in both habitat and fish assemblages, which may prevent any correlative patterns between habitat loss and fish assemblages being observed.

As seagrass declines within an area, fish may use alternative nursery habitats. Where such a habitat shift occurs, seagrass loss will result in no concomitant loss of fisheries (but see Hughes et al., 2002). For example, new settlers of red drum (*Sciaenops ocellatus*, Sciaenidae) are still found within the Galveston Bay system of Texas despite seagrass cover declining by 80% during the previous 30 years (Fuls and Hensley, 1998, cited in Stunz and Minello, 2001). New settlers may be utilizing salt marsh, oyster reef, or non-vegetated habitats.

Small-scale experiments where the canopy of seagrass is removed may also be used to investigate the effect of seagrass loss on fishes (e.g. Connolly, 1994b; Guidetti and Bussotti, 2002). Connolly (1994b) found that abundances of fish were only slightly reduced by the removal of seagrass, whereas Guidetti and Bussotti (2002) found no differences in total fish abundance and species richness, but a significant difference in species composition and relative abundance of some species with seagrass removal. Fish assemblages did, however, differ between seagrass and non-vegetated habitats (including the habitat in which seagrass was removed), as well as between seagrass removal and non-vegetated habitat suggesting that some factor other than seagrass canopy may also be important (Guidetti and Bussotti, 2002). Rapid regrowth of seagrass is a limitation of such experiments. Removal experiments can only be conducted for short periods of time (e.g. 10–14 days) or continual seagrass removal is required. Disturbances due to seagrass removal and the small spatial scale of experimental manipulations also are limitations for such experiments.

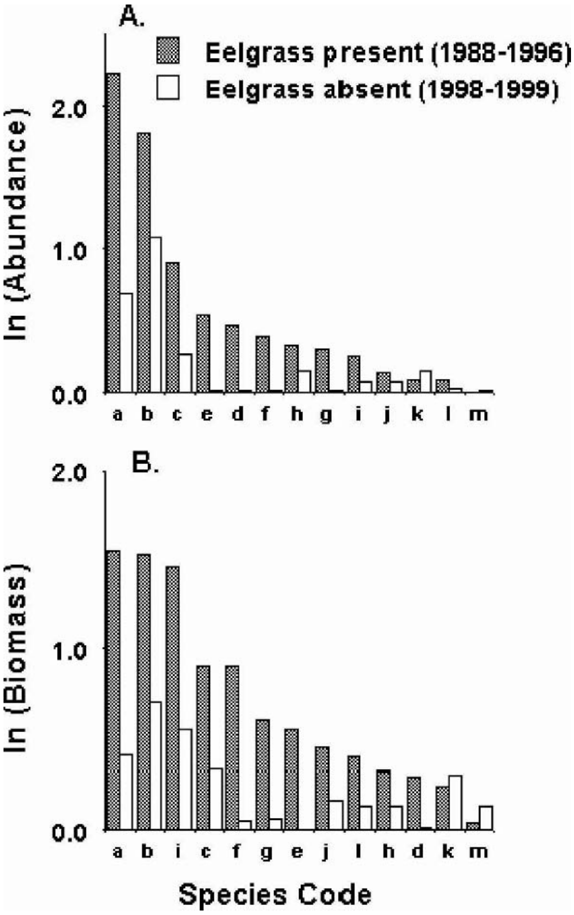

Fig. 6. Mean abundance and biomass per 100 m^2 of 13 common species in Waquoit and Buttermilk Bays (Cape Cod, Massachusetts, USA) in years when seagrass (*Zostera marina*) was present at some sites (1988–1996), and when seagrass had disappeared completely (1988 and 1999). Species are arranged from most to least numerically abundant. From Hughes et al. (2002). Reproduced by permission of Estuarine Research Federation.

Manipulative experiments are difficult to perform at meaningful scales and often are regarded as socially unacceptable (Nagelkerken et al., 2001; Vanderklift and Jacoby, 2003). When events result in loss of seagrass, these perturbations should be used as an opportunity for experiments (see for example, Underwood, 1996).

B. Correlations Between Seagrass Cover and Fisheries Catch

Several studies have reported a significant, positive linear relationship between commercial landings of penaeid shrimp and the area of vegetated wetlands, but similar correlations generally have not been shown for other species (see references within Orth and van Montfrans, 1990). Orth and van Montfrans (1990) found no significant relationship between landings of blue crab (20 year averages) and habitat quantity (total seagrass, total marsh, or total vegetated area) across broad latitudinal distances (four major regions of the USA), but similar comparisons within the Gulf of Mexico showed a significant positive relationship of blue crab landings with total vegetated area. When a log-linear regression model was used to estimate the relationship between catch per unit effort of blue crab and abundance of submerged aquatic vegetation (SAV) in the previous year the relation between catch per unit effort (CPUE), SAV lagged by 1 year, effort and time was highly significant suggesting a relationship between seagrass cover and subsequent blue crab catches (Anderson, 1989). Although there are problems with using fishery dependent landings, few fisheries-independent data are available to use for making comparisons.

The relationship between seagrass habitat and fisheries production has also been investigated in terms of the possible use of seagrass as a nursery, feeding, or spawning area by fish. A seagrass residency index (SRI) was constructed, which modeled residence time of particular commercially and recreationally important fish in seagrass habitats in South Australia (Scott et al., 2000). The SRI indicated that garfish (*Hyporhamphus melanochir*, Hemiramphidae) and King George whiting (*Sillaginodes punctata*, Sillaginidae) were more likely to be affected by changes in abundance of seagrass beds than Australian salmon (*Arripis truttacea*, Arripididae) or snapper (*Pagrus auratus*, Sparidae). A SRI was the first step toward developing a spatial model of seagrass–fish habitat that would allow quantitative assessment of the economic value of seagrass habitats, particularly for fisheries production (Scott et al., 2000).

C. Trophic Linkages

Many of the small fish which are found in seagrass beds may be important prey for species utilizing other habitats. For example, more than 30% of the 93 fish species sampled from a variety of habitats in Groote Eylandt (Gulf of Carpentaria, Australia) were primarily piscivorous with the main fish species consumed being Mugilidae, Clupeidae, and Monacanthidae (Brewer et al., 1995). However, few studies have sampled both predatory fishes and their prey over the same spatial and temporal scales. Abundances of small fishes were negatively correlated with the abundances of a transient piscivorous fish *Arripis truttacea* (Arripididae) over the same temporal scales (Hindell et al., 2000b). Based on the diet of *A. truttacea*, Hindell et al. (2000b) suggested that piscivory may influence the assemblage structure of small fishes in seagrass beds. They also investigated the influence of predatory fish on the abundance of small fish in seagrass (structured) and non-vegetated (unstructured) habitats by manipulating the presence of piscivorous fishes using exclusion and enclosure cages (Hindell et al., 2000a). When predators were excluded, the relative increase of small fish was greater over non-vegetated habitats than seagrass, suggesting that the structural complexity of the seagrass may somehow mediate predation (Hindell et al., 2000a, 2002). At the level of an individual species, predation strongly influenced the distribution of King George whiting (*Sillaginodes punctata*, Sillaginidae) within a location, but this was likely a behaviorally mediated response rather than direct predation (Hindell et al., 2002). Experiments were conducted at multiple ($n = 3$) locations within an estuary (Port Phillip Bay), but the results differed among locations. For example, at one location predation was not important, but at another there was a strong predation effect (Hindell et al., 2001). These results were thought to reflect differences in abundances of predatory fish between the two locations.

In another experimental study, Eggleston et al. (1998b) investigated trophic links between seagrass and patch reefs within a large seagrass bed in the tropics. Prior to deployment of patch reefs, densities of crabs were similar at experimental and control sites. After deployment, the density of crabs was reduced by one-half to 43-fold, whereas densities of Nassau grouper (*Epinephelus striatus*, Serranidae) increased. Predators associated with patch reefs, thus, had a significant impact on nocturnally foraging crabs in adjacent seagrass meadows. The results of this study highlight an important trophic link between seagrass habitats and tropical patch reefs.

D. Tracing the Contribution of Seagrass Production to Fisheries Species Elsewhere Using Stable Isotopes

Seagrass beds may indirectly support species in other areas. Studies tracing the contribution of seagrass to fisheries species outside of seagrass habitats have focused on analysis of stable isotopes. Initial studies used a single isotope (e.g. $\delta^{13}C$), but later work used two or more isotopes. First-feeding larval blue grenadier (*Macruronus novaezelandiae*, Merlucciidae) were found to be part of a microbial planktonic food chain that was based on seagrass detritus, which is exported offshore during storm events (Thresher et al., 1992). Seagrass detritus also may be important in the food chain of prawns collected from offshore waters, although based on the $\delta^{13}C$ values the primary food source could also be benthic microalgae or a mixture of seagrass and plankton (Loneragan et al., 1997).

Using multiple stable isotopes may be particularly powerful for tracing trophic relationships in coastal waters (Moncreiff and Sullivan, 2001). Surprisingly, few studies have used a multiple stable isotope approach (e.g. $\delta^{13}C$, $\delta^{15}N$, $\delta^{32}S$) to study food webs in seagrass systems (see Mateo et al., Chapter 7). The trophic relationships of fish and invertebrates on the continental shelf of southeastern Australia were examined using stable isotopes of carbon and nitrogen (Davenport and Bax, 2002). Although the results of this study showed that the main source of primary production was oceanic phytoplankton, there was some evidence that seagrass contributed to the benthos because benthic invertebrates had $\delta^{13}C$ values intermediate between particulate organic matter and seagrasses (Davenport and Bax, 2002). Multiple stable isotopes have also been used to show that seagrass material contributes substantially to fisheries species found over adjacent non-vegetated habitats (Melville and Connolly, 2003).

E. Juveniles Moving from Seagrass to Other Habitats

Fish may move between habitats either through the dispersal of pelagic larvae or by the movements of juvenile or adult fish between habitats. After settling in seagrass habitats, the juveniles of reef species must move from seagrass to reach coastal reefs. Where juveniles are found in seagrass as well as other habitats, the relative contribution of different habitats to adult populations needs to be determined. A recent paper reviewed movement from juvenile to adult habitats and the usefulness of different methods for determining movement (Gillanders et al., 2003). Most studies have used either changes in abundance of organisms among separate habitats or a progression of size classes among the separate habitats to infer movement from juvenile to adult habitats (e.g. Gunderson et al., 1990; Gillanders, 1997).

A few studies have used mark-recapture methods (e.g. Ruello, 1975, 1977; Koutsikopoulos et al., 1995), although in many cases such studies examined movement of juveniles from estuaries rather than seagrass per se. Artificial tagging methods, although providing good evidence for movement, are difficult to implement in many cases due to the small size of fish in seagrass beds, the high mortality rates of juveniles (e.g. Hixon, 1991) and low rates of recapture of tagged fish (e.g. Sheaves, 1995). Large numbers of organisms must be tagged to produce even low numbers of recaptures. Recent developments with internal artificial tags (e.g. coded wire tags, CWT; visible implant fluorescent elastomer, VIF) show promise as tools for determining movement. Fish as small as 8–11 mm standard length have been tagged on coral reefs using internal tags (Beukers et al., 1995); the tags show relatively long retention times (several months) and few biological side effects. The feasibility of using these tags may depend on the visibility of the tags over long time periods (e.g. 1–2 years). Juvenile organisms grow fairly rapidly, and therefore it is possible that growth of surrounding tissue may limit visibility of tags. In addition, use of CWT and VIF tags will require individual handling of fish, which may be difficult for some species due to high mortality rates. I am not aware of any studies that have used CWT or VIF tags to track movement of organisms from juvenile seagrass to adult habitats. Remote sensing capabilities that do not rely on recapture per se are an advance over mark-recapture techniques, but are not suitable for tracing movements of most species (Hobson, 1999).

More recently, researchers have used tissue assays and related these to geographic areas to investigate animal origins and movement (Hobson, 1999). One such method employs the use of stable isotope ratios (review: Peterson and Fry, 1987). Animals acquire a natural isotopic tag (or label) from their diet (e.g. carbon). Animals that move between isotopically distinct feeding habitats can retain isotopic information for varying periods of time, depending on the turnover rate for the tissue of interest (Hobson, 1999). Fry (1981) measured the δ^{13}C values of migrating brown shrimp (*Farfantepenaeus aztecus*, Penaeidae) to determine which habitats shrimp originated from and to determine which habitats contributed most to the commercial shrimp fisheries. Such an analysis is dependent on differences in isotopic signatures between feeding grounds (e.g. seagrass meadows and phytoplankton-dominated open bays). Seagrass beds had isotopic signatures that were distinct from open bay areas. As shrimp moved offshore from estuaries, they metabolized away the estuarine carbon in their tissues as they foraged offshore (Fry, 1981). Non-migratory offshore shrimp had constant values of δ^{13}C that was similar across the three areas sampled. Migrating shrimp will rapidly become indistinguishable from resident shrimp. The effective offshore life of the estuarine tag was predicted to be about 1.1–2.9 months for female and male shrimp, respectively (Fry, 1981). Shallow water habitats such as seagrass meadows were important contributors of shrimp to commercial fisheries. As with food web studies, the utility of this method is limited by the number of habitats that are distinguishable, although additional isotopes (e.g. hydrogen, nitrogen, sulfur) may allow more habitats to be distinguished. The method also is limited by the growth rate and rate of tissue turnover of target species (e.g. Fry, 1983).

In a similar study, the contributions of seagrass and mangrove habitats to the offshore pink shrimp (*Farfantepenaeus duorarum*, Penaeidae) fishery were estimated using carbon and nitrogen stable isotopes (Fry et al., 1999). Shrimp from seagrass had ^{13}C-enriched values that were distinct from the values of animals from mangrove-lined bays. It was suggested that 75% of shrimp at each location were residents because their isotopic composition was within a ±1‰ range for carbon and nitrogen isotopes, and that the remaining 25% were transient migrants because their isotope composition fell outside this range (Fry et al., 1999) (Fig. 7). In the offshore fishery, 40% of small shrimp were classified as recent immigrants and the majority of these had isotope values consistent with a seagrass origin (Fry et al., 1999) (Fig. 7).

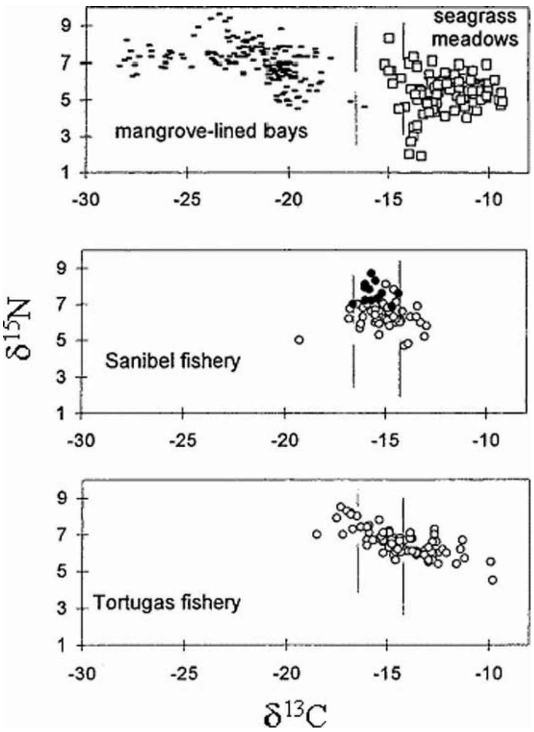

Fig. 7. Isotope distributions of pink shrimp from inshore (seagrass and mangroves) and offshore locations (Sanibel and Tortugas fisheries, southwest Florida Shelf, USA). Inshore shrimp were collected from seven seagrass sites and 12 sites in mangrove-lined bays (top panel). Vertical lines show the δ^{13}C range for 12 large (>20 g wet wt; solid dots in middle panel) pink shrimp collected from the Sanibel fishery. Since the inshore isotope tag will be turned over and lost once shrimp move offshore these animals were used to define the normal δ^{13}C range for animals that had lost their inshore isotopic tag and were considered resident offshore shrimp. Values outside this range indicate a recent origin from inshore habitats. The δ^{13}C signature of shrimp from both fisheries was more similar to those found in seagrass meadows rather than mangrove-lined bays suggesting recruitment into the fishery from seagrass meadows. From Fry et al. (1999). Reproduced by permission of Bulletin of Marine Science.

Calcareous structures in fish, such as otoliths (ear bones), can also be used to determine origins and movements of fish. Although not utilizing seagrass, the natal origins of Atlantic salmon (*Salmo salar*; Salmonidae) have been determined using δ^{87} Sr. An isotope approach was possible because the majority of rearing streams differed in their δ^{87} Sr signatures (Kennedy et al., 1997). Fish take up Sr isotopes in direct proportion to their availability in water and substitute Sr for Ca in calcified tissues during growth (Hobson, 1999). The Sr isotopic composition of fish otoliths is about the same as that of stream water because Sr does not fractionate during assimilation (Hobson, 1999). A similar approach may be possible for determining origins of fish from seagrass beds in different regions or to determine the relative contribution of different habitats to adult populations. It will, however, be necessary to determine the spatial and temporal scale of isotopic differences prior to determining links between habitats.

Elemental signatures (e.g. Sr, Mn, Ba) in the otoliths of fish have also been used to evaluate contributions of larval/juvenile habitats to adult stocks (e.g. Gillanders and Kingsford, 1996; Swearer et al., 1999; Thorrold et al., 2001; Gillanders, 2002). Because of the acellular and metabolically inert nature of otoliths, many of the elements that are used as a natural tag and accreted onto the growing surface of the otolith are permanently retained (see review: Campana, 1999). Otoliths continue to grow through time ensuring that the entire lifetime of a fish has been recorded, and differences in chemistry between layers of an otolith can be resolved to within days or years of their deposition. The calcium carbonate and trace elements that make up 90% of the otolith are derived primarily from the water (Milton and Chenery, 2001), although in practice physiological filters likely ensure that there is not a simple linear relationship between the water and the otolith (Campana, 1999). Similar approaches have recently been investigated using calcified structures of crustaceans (e.g. Dibacco and Levin, 2000) and molluscs (e.g. Zacherl et al., 2003).

The only study that has used elements in otoliths to determine links between seagrass habitats and other habitats was that of Gillanders and Kingsford (1996). Significant differences were found in the elemental signatures of otoliths of juvenile blue groper (*Achoerodus viridis*; Labridae) collected from two habitats, seagrass, and rocky reef. The central region of adult otoliths corresponding to that laid down when the fish was a juvenile was then analyzed to determine the relative importance of the two juvenile habitats in supporting adult stocks and to demonstrate links between juvenile and adult habitats. Their results suggested that while seagrass habitats contributed to adult populations in terms of numbers of fish, rocky reef habitats were also important. A similar approach should be possible for other species.

VII. Conservation and Management Issues

A. General Observations

Interest in conservation biology within the marine area is expanding rapidly as the effects of overfishing, pollution, habitat destruction and fragmentation, invasive species, and global climate change impact marine systems (Ruckelshaus and Hays, 1998). Dramatic losses of seagrass habitats have occurred worldwide due to direct impacts, but frequently indirect effects on fish and invertebrates within seagrass habitats (see Section VII.C of this chapter) also are common. In order to mitigate against loss of seagrasses, many restoration projects have been undertaken and the information obtained on the use of restored seagrass by fish (see Section VII.C of this chapter) is now available. A broad-scale approach to management of seagrass is necessary, but no detailed studies exist that identify suitable indicators of seagrass health (see Seagrass "health" and fisheries, Section VII.D).

B. Impacts Due to Fisheries

The impacts of fishing gear (e.g. mechanical dredges, hydraulic dredges) on seagrass systems have been described as resembling 'the effects of terrestrial ploughs in that plants are uprooted and dispersed or buried' (Blaber et al., 2000). Direct impacts on seagrass beds are likely to vary depending on the type of gear used. The mechanical harvesting of clams is particularly devastating. Mechanical clam harvesting in seagrass beds is done by modifying boat engines so that the propeller wash is directed downwards (as opposed to backwards), and in shallow water the action of the propeller suspends bottom sediments and clams into a plume in the water column (Peterson et al., 1987). The suspended clams (*Mercenaria mercenaria*, Veneridae) are then collected by a trawl net towed behind the boat. A field experiment was used to examine the effects of clam raking (hand raking while walking across the seagrass) and two different intensities of mechanical harvesting of clams ('clam kicking') on recruitment of clams, biomass of seagrass, density of benthic macroinvertebrates, and density of bay scallops (*Argopecten irradians*, Pectinidae) in both seagrass and sand flat habitats (Peterson et al., 1987). Clam harvesting did not affect the density or species composition of benthic macroinvertebrates, but led to substantial decreases in seagrass biomass, a potentially negative impact on recruitment of hard clams, and a reduction in abundance of bay scallops. Recovery of seagrass biomass occurred within 1 year in the raking and light clam-kicking treatments, but seagrass biomass was still around 35% lower than predicted from controls after 4 years in the intense clam-kicking treatments (Peterson et al., 1987). Intense mechanical clam harvesting in vegetated areas also may have impacts on commercial fisheries, as seagrass biomass is likely to decline.

Trawling differs from dredging in that trawls are dragged on or near the bottom (Dayton et al., 1995). Although habitat damage by trawling is not a major issue in estuarine or nearshore areas other than in the tropics (Blaber et al., 2000), it has been reported to destroy *Zostera marina* in Scotland (Northridge, 1991, cited in Dayton et al., 1995) and *Posidonia* beds in the Mediterranean (Dayton et al., 1995; Sanchez-Jerez and Ramos-Espla, 2000). The predominant means by which trawling eliminates *Zostera* is by altering sediment type (Dayton et al., 1995). In the southwest Mediterranean, boats often illegally trawl over *Posidonia oceanica* meadows and cause physical degradation of the habitat. Sanchez-Jerez and Ramos-Espla (1996) investigated the effect of bottom trawling over seagrass habitat on seagrass characteristics, and fish and invertebrate assemblages. Although they compared two sites 6 km apart (one trawled and one untrawled area) and their results therefore could reflect spatial variation between sites, they did find differences in density and assemblage structure of fishes between the trawled and untrawled areas. At coarse levels of taxonomic resolution significant differences in assemblage structure of invertebrates could not be detected, but at finer levels (e.g. family and species) amphipods and isopods showed significant differences between trawled and untrawled sites (Sanchez-Jerez and Ramos-Espla, 1996). To reduce the impact of trawling in the Mediterranean, anti-trawling artificial reefs have been deployed. Such reefs were shown to change the assemblage structure of fishes at a scale of tens to hundreds of meters, mainly because reef-associated species congregate around them (Sanchez-Jerez and Ramos-Espla, 2000).

Roller beam trawls are used to capture live shrimp (primarily pink shrimp, *Farfantepenaeus duorarum*, Penaeidae) in seagrass beds of Florida. These shrimp are used as bait in the recreational fishery. Although these trawls are designed to roll over the bottom, they may break off and collect leaves of seagrass (Meyer et al., 1999). No significant reduction in mean shoot density, number of blades per shoot, longest blade length per shoot, total blade length per shoot, and above and below-ground biomass was detected with four levels of trawling (1, 3, 9, and 18 trawls) (at nine areas with Tampa Bay, Florida, USA) suggesting that roller beam trawls have minimal impact on seagrass habitat (Meyer et al., 1999). However, potential effects of fishing are likely to be highly dependent on statistical power (Peterman, 1990). Despite minimal impact on seagrass, 42 species of fish were caught by the trawl, and these showed variable (0–100%) rates of survival; small fish were significantly more susceptible to trawl-induced mortality than larger fish (Meyer et al., 1999). Because trawling-induced mortality was found to differ among species, roller beam trawling may alter species diversity and composition.

Commercial harvesting of bay scallops (*Argopecten irradians*, Pectinidae) is done principally by using a boat to tow heavy epibenthic gear, whereas recreational and small-scale commercial harvesters use hand collecting, hand-pulled dredges, and raking to take scallops (1984). Scallop harvesting may therefore impact the seagrass habitat itself. Fonseca et al. (1984) found that as dredging effort increased, the number of seagrass shoots and seagrass dry weight per core also decreased. These impacts are likely to have implications for the habitat itself, as well as settlement of scallop larvae.

Many juvenile animals are taken as by-catch by fishers in estuaries and shallow waters. Pink shrimp (*Farfantepenaeus notialis*, Penaeidae) are intensively exploited using small-mesh nets in West African lagoons and estuaries. Along with these shrimp vast numbers of non-marketable juvenile fishes also are captured, including juveniles of valuable fisheries (Blaber et al., 2000). Although large numbers of juveniles are removed, the quantitative impact on the estuarine fish community and of the artisanal fishery for adults is unknown (Blaber et al., 2000). Juvenile fish also may be collected from estuaries for export in the ornamental fish trade. For example, *Monodactylus argenteus* (Monodactylidae) and *Scatophagus argus* (Scatophagidae) are collected in Sri Lanka for the ornamental fish trade and *Epinephelus tauvina* (Serranidae) is exported to south-east Asia for fattening (Pinto and Punchihewa, 1996). In Sri Lanka, collecting fish and invertebrates is thought to damage seagrass habitat; restrictions on collecting organisms do not exist (Pinto and Punchihewa, 1996), and the effect of these activities on fish stocks is unknown.

Aquaculture ventures, in particular fish farming, may also affect the distribution of seagrass in some areas, largely due to organic wastes that are released into the water column (Delgado et al., 1999; Cancemi et al., 2003). For example, Ruiz et al. (2001) found that since the onset of fish farming 53% of the former seagrass meadow (*Posidonia oceanica*) had either been completely lost or significantly degraded. In another study, although fish farming at one site had ceased, seagrass decline persisted possibly due to excess organic matter in the sediment (Delgado et al., 1999). Further studies are needed on the impacts of fish farming on seagrasses.

Some indirect effects of fisheries on seagrass habitats include propeller scarring by boats navigating to and from fishing operations, trampling of seagrass (e.g. hand raking for clams), raising turbidity levels, and altering sediment type. The abundance and size distribution of pinfish (*Lagodon rhomboides*, Sparidae) and pipefish (*Syngnathus scovelli*, Syngnathidae) did not differ between propeller-scarred (characterized by up to 31% vegetation loss) and reference seagrass beds (Bell et al., 2002). Thus, in areas that have been moderately to intensively scarred, loss of seagrass did not appear to affect populations of fish (Bell et al., 2002). Similar results of no effect were found for shrimp where scarring impacted up to 50% of the habitat (Bell et al., 2002). Large areas of non-impacted seagrass in the vicinity of propeller-scarred areas may provide an alternative habitat for organisms. Propeller scarring may also have more of an effect on sedentary and infaunal species. Further research is required to determine whether the results of Bell et al. (2002) are applicable to other areas.

C. Restoration of Seagrass and Fisheries

With continued loss of seagrass beds and potential implications of this habitat loss for fisheries resources, restoration of seagrass habitats could prove important. Effective restoration of habitats depends on planted or restored seagrass beds providing resources that are similar to natural beds (Fonseca et al., 1990, 1996). Despite this, commonly used indicators of seagrass recovery typically focus on the seagrass itself (e.g. % cover) and fish and invertebrates may not be monitored. Although many studies have shown that fish and crustaceans utilize natural seagrass beds, remarkably few studies have examined whether restored or created seagrass beds provide important habitat and food resources for fish species. Transplanted, recently seed-colonized, and natural beds of seagrass showed similar numbers and species of fish and shrimps within 2 years of planting (Fonseca et al., 1990, 1996). Areas that were planted with seagrass were initially colonized by adults and subsequently by recruitment of early life history stages. Whether these results obtained for the first 3 years since planting can be extrapolated across greater temporal scales is unknown (Fonseca et al., 1996). The abundance and species of animals (fish and invertebrates) in restored areas and an unaffected control site were similar but differed from a nearby barren area that had never recovered (McLaughlin et al., 1983).

In a natural experiment, the fishes of seagrasses that recolonized around disposal islands (the latter were created when the Atlantic Intracoastal Waterway was dredged) and those of natural seagrass beds were compared. Differences were found in the fish assemblages of well established recolonized meadows and natural meadows, whereas newly recolonized meadows and natural seagrass meadows had similar assemblages (Brown-Peterson et al., 1993). Members of schooling, mobile families of fish (Clupeidae, Engraulidae, Atherinidae, Mugilidae) were more common in recolonized meadows, whereas benthic, sedentary families (Syngnathidae, Gobiidae) were more common in natural meadows (Brown-Peterson et al., 1993). Seagrass species composition of the recolonized (characterized by *Halodule wrightii*) and natural (composed of a mixture of *H. beaudettei* and *Cymodocea filiformis*) meadows also differed, however, and this may have caused differences in fish assemblages between the two types of seagrass.

Growth, survival, and movement of organisms have infrequently been investigated in restored seagrass areas (but see Kenworthy et al., Chapter 25; Bell et al., Chapter 26). Some data from marsh habitats is available that shows no difference in growth rates between restored and reference marshes and that both types of marsh are utilized by young-of-the-year fish (Miller and Able, 2002).

Table 4. Sequence of steps needed for scientific development and validation of an indicator.

Step	Relevant questions arising
(1) A monitoring need is perceived	Is it recognized by scientists and/or managers?
(2) Hypothesized relationship	What links an indicator to an impact?
(3) Scientific feasibility	Is it worth persisting with?
(4) Experimental laboratory trials	Under what range of conditions does it perform?
(5) Field validation	What practical signal is recovered?
(6) Management-scale, on-site assessment	Is it routinely implementable?
(7) Develop feedback loops	Are there appropriate management responses?
(8) Protocols for implementation	How best can it be disseminated and accessible?
(9) Verification	How effective is it in use?
(10) Refinement	How can it improve with advancing knowledge?

Source: Fairweather (1999) Determining the 'health' of estuaries: Priorities for ecological research. Reproduced by permission of Blackwell Publishing.

D. Seagrass 'Health' and Fisheries

Ecosystem health has been defined in terms of resilience (a system's capacity to maintain structure or function in the presence of stress), organization (diversity and number of interactions between system components) and vigor (activity, metabolism or primary productivity) (Rapport et al., 1998). Fairweather (1999) discusses the role of indicators for ecosystem health in estuaries and provides information from a pilot study conducted on mangrove ecosystems near Sydney (New South Wales, Australia). I am not aware of a similar study assessing health of seagrass ecosystems, although Edwards et al. (2001) examined metals in seston (organic and inorganic particulate matter) and flesh of commercial fish species from contaminated and uncontaminated coastal sites in South Australia to determine if a correlation between metal levels and biochemical and cytogenetic effects in fish exists. High levels of metals (cadmium, lead, and copper) were found in seston and fish, and these were correlated with biomarkers. Such an approach may be useful in monitoring marine pollution. However, this study examined few potential indicators of functioning within seagrass ecosystems and was conducted at only three sites. An approach similar to that adopted by Fairweather (1999) in which multiple indices are developed and a sequence of steps for development and validation of an indicator are followed could be especially useful for seagrass ecosystems (see Table 4). Seagrass ecosystems should be incorporated into large-scale programs addressing the health, functioning, and sustainable use of coastal systems (Duarte, 1999; Epilogue, this volume).

VIII. Future Research Directions

A. Broadscale Studies

Although a number of studies have compared abundance of organisms in seagrass with one or two other nearshore habitats, relatively few studies have compared abundances, growth, and survival across a range of nearshore habitats and at multiple locations. Such information is vital for determining the potential effects of seagrass loss on marine organisms. If, for example, species are able to utilize a wide range of habitats, then loss of seagrass may have less effect than if species utilize only seagrass. All life history stages must be included in such studies. For example, seagrass may be the only habitat in which a species spawns. Future studies used to quantify fish and invertebrate abundance should use similar methods and provide estimates of the sampling efficiency of the gear used in different habitats. They should also consider possible variation due to differing tidal levels. In addition, comparisons of growth and survival among the different nearshore habitats are needed. Several studies have suggested that abundance may not vary among habitat types, but that growth and survival may differ (e.g. Tupper and Boutilier, 1995).

B. Among Patch and Landscape Scales

Although a number of studies have focused on within-patch dynamics (e.g. shoot density, shoot biomass), few studies have focused on among-patch variables, and most of this research focuses on the effects of habitat fragmentation. Even fewer studies, particularly on commercially important fish species, have been conducted at the landscape scale, even though seagrasses are ideal systems to use to address landscape scale questions (Robbins and Bell, 1994). Further studies are clearly needed to investigate how the configuration of the habitat (e.g. patch size, patch isolation, proximity to edge), amount of habitat (e.g. habitat cover), and adjacent habitats (e.g. non-vegetated areas, mangroves) may influence not only abundance of organisms within seagrass but also their growth, survival, and movement patterns. Structural characteristics of the seagrass habitat (e.g. shoot density, shoot biomass) often vary at the among patch and landscape scale; for example, structural complexity is often positively correlated with seagrass patch size (Hovel, 2003; Bell et al., Chapter 26). In addition, seagrass cover and configuration of habitat also may covary (Hovel, 2003). Covariation of variables at a range of spatial scales creates problems for comparisons of the effects of different variables. Such problems can be overcome either by using artificial habitats (e.g. McNeill and Fairweather, 1993) or by statistically removing the covariation (e.g. Hovel, 2003). Use of artificial habitats may, however, not be possible at the landscape scale.

Elements of seagrass habitat structure at more than one scale may influence abundance, growth, and survival of organisms, thus multi-scale approaches are required (see Bell et al., Chapter 26). It will also be necessary to determine both the direction and magnitude of influence of different variables and how these vary at regional and biogeographic scales. Simultaneous sampling and experiments over broad spatial and temporal scales are required. In addition, the scale at which studies have been conducted has varied (Villard et al., 1999; Hovel, 2003). Future studies should consider biological information on the species being investigated (e.g. dispersal capabilities, foraging behavior, home range) and factor this information into the choice of scales at which to measure responses to habitat structure. For example, studies on wide-ranging species should be conducted at a larger scale than those focusing on infauna of seagrass beds.

C. Regional and Biogeographic Scales

At regional and biogeographic scales, a variety of sampling designs and methods have been utilized making comparisons among studies difficult. A global approach, where researchers around the world conduct experiments across similar temporal and spatial scales using the same design and methodology, although ambitious, could be extremely useful for determining generality of patterns. Such an approach has recently been used to determine the impact of natural UV-radiation on shallow marine hard-bottom assemblages (Wahl, Kiel University, Germany; personal communication).

D. Seagrass Loss and Fisheries

Few clear examples exist of the demise in fisheries catches when seagrass has been lost from an area. The great wasting disease of eelgrass in the North Atlantic in the 1930s, and its effects on fisheries are still the subject of much debate (see Duarte et al., Chapter 11, Moore and Short, Chapter 16 and Kenworthy et al., Chapter 25). As seagrass declines within an area, fish may use alternative habitats. Examining the link between habitat and fisheries requires monitoring of both catch and seagrass cover prior to episodes of seagrass loss and following recovery. Data on both catch and seagrass cover are currently unavailable for many areas. In addition, changes in organisms inhabiting seagrass before and after seagrass loss are poorly known (Connolly et al., 1999). Areas that have lost seagrass may also go through a range of habitat successions, but further information is required on what habitats occur in areas where seagrass is lost and how the assemblage structure may change as a consequence. Baseline studies within seagrass beds should encompass not only sufficient spatial scales, but also sufficient temporal scales such that natural site-to-site and annual variability can be considered enabling useful comparisons after seagrass loss (Hughes et al., 2002). Events that result in loss of seagrass should be seen as opportunities for natural experiments. Few datasets of a sufficient time frame exist to enable adequate modeling of the relationship between fisheries catches and seagrass cover (or some variable encompassing the amount of seagrass in an area). Further work in this area is required.

Few studies have attempted to model the effects of seagrass removal on fishery species. Despite a lack of studies, it should be possible to use past data and potentially describe future states. Initial model fitting should adequately describe the data, but will also require independent tests of the assumptions and the importance of particular variables (Haddon, 2001).

E. Links between Seagrass and Fish

Trophic links between seagrass and other habitats (e.g. coral reefs, non-vegetated), particularly involving commercially important species preying on small non-commercial species, are only just starting to be investigated. Further studies are required that sample both predatory fishes and their prey over the same spatial and temporal scales. Such studies should also incorporate dietary analysis of piscivorous fish. Isotope studies may be particularly useful in this area. Stable isotopes may also help trace the contribution of material from within seagrass beds to fishery species elsewhere (e.g. Thresher et al., 1992). If seagrass material is being utilized and assimilated by species elsewhere, then this may have implications for loss of seagrass. At present, the importance of exported seagrass material to organisms in other habitats is poorly known.

Links between seagrass habitats and other habitats are still poorly known. In particular no studies have examined the contribution of seagrass beds from different estuaries or regions to commercial fisheries (e.g. Gillanders, 2002) and few studies have examined the contribution of differing juvenile habitats to adult populations (e.g. Gillanders and Kingsford, 1996). Likewise, few if any studies have examined relative differences in the contribution of larvae from different regions to seagrass beds. Thus, larval sources and transport pathways are completely unknown. With developments in the field of isotopic and elemental chemistry, determining origins, movement, and contributions from different areas/habitats should be possible. This approach requires empirical determination of spatial and temporal differences in chemistry over the range of the organism of interest. Depending on spatial and temporal differences in chemistry it may be necessary to track adults back to the cohort of recruits from which they originated (e.g. Gillanders, 2002). Once seagrass beds that contribute more individuals to adult populations are identified it will then be possible to focus conservation strategies (e.g. estuarine protected areas) on these areas.

F. Larval Studies

Further information is required on larval dynamics which should enable a better understanding of larval supply processes (see above). All aspects of the biology and ecology of larvae (of fish found within seagrass beds) require further study. In many cases, even the taxonomy of larvae is poorly known. Larval behavior has only recently been examined but there is still much work to be done. While larvae are able to control where they are and where they will settle, it is not known at what stage they assume this control. One of the limitations of many larval studies is that extensive sampling then requires considerable effort to process samples. Methods that overcome such limitations are required (e.g. molecular techniques).

G. Impacts of Fishing

Impacts of fishing on fish stocks and seagrass habitats have been investigated in some areas of the world, but have been largely unexplored in other regions (e.g. Africa, Asia). Although a number of studies have investigated by-catch of fishing gear and altering gear to reduce by-catch, few of these studies have focused specifically on seagrass habitats or determined potential mortality rates of fish returned to the water. Investigations of fishing-induced mortality and how this varies by species, size of fish, and gear type are needed. Such information combined with by-catch data would enable us to determine the quantitative impact of fishing on fish within seagrass habitats. The indirect effect of fishing on seagrass inhabitants also requires further investigation. For example, the effects of propeller scarring (e.g. Bell et al., 2002) and trampling in seagrass (e.g. Eckrich and Holmquist, 2000) on faunal assemblages have only recently been investigated. A range of manipulative experiments have examined sediments and turbidity within seagrass, but few studies have focused on seagrass inhabitants. Thus, further research that investigates both the direct and indirect effects of fishing on seagrass inhabitants, including commercially important species is needed. Such research needs to be done for a range of seagrass species.

H. Seagrass Restoration and Fisheries

Much literature is appearing on restoration of seagrass habitats (e.g. see chapters within this book), but few studies investigate whether planted or restored seagrass provides similar resources to natural seagrass. Studies that monitor the effectiveness of planted/restored seagrass should monitor not just the plants themselves, but also the inhabitants, and whether there are differences in food resources, growth, and mortality of organisms between natural and restored seagrass. Such studies would ideally require experimental designs that include multiple restored and control areas. Further studies on evaluating restoration efforts in terms of the organisms present would then help determine whether it is reasonable to remove seagrass beds for development and replant in other areas.

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Chapter 22

Predation in Seagrass Beds

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I. Introduction

The ability of leaves, roots, and rhizomes to reduce the rate of predation on associated animals is as well studied as any topic having to do with seagrass beds, and is one of the major tenets of the seagrass 'nursery role hypothesis' (Beck et al., 2001). The past two decades have each produced detailed reviews of the effects of seagrasses on the outcome of predator–prey interactions (e.g. Heck and Orth, 1980; Orth et al., 1984; Heck and Crowder, 1991; Orth, 1992; Bartholomew et al., 2000; Hemminga and Duarte, 2000; Williams and Heck, 2001). In addition, Duffy and Hay (2001) have written a comprehensive overview of consumer–prey relationships in marine environments. Although the major conclusions of these reviews, that seagrass leaves, roots, and rhizomes reduce the rate of predation on both mobile and sessile animals, whether they are infaunal or epifaunal, have remained unchallenged, new issues have been raised. In this chapter, we first summarize the previous generalizations that continue to be supported by recent work, and then focus attention on results that challenge the conventional wisdom on predator–prey interactions in seagrass meadows. Throughout, we provide suggestions for studies that seem to be capable of resolving controversies or breaking new ground.

II. Effects of Seagrasses on Predator–Prey Interactions in Ecological Time

By far, the greatest attention has been focused on how seagrass biomass, surface area, and physical structure (principally estimated by shoot density) influence the outcome of predator–prey interactions among epifaunal macro-organisms. All this work has been concerned with events occurring on ecological time scales, that is, lasting from a few hours to a few generations for the predators and prey being studied. Motile, macro-epifauna (e.g. amphipods, crabs, shrimps) have been emphasized in these studies because they are the most conspicuous components within the seagrass canopy and because it is easier to study epifaunal macrofauna than epifaunal micro- or meiofauna, or infauna of any size. Also, a few of these species are commercially valuable and funding has been available for elucidating the factors that determine their survival, e.g. blue crabs, spotted seatrout, prawns, lobsters (see Heck et al., 2003). As intuition and observations suggested to earlier investigators, and a recent meta-analysis of experimental data has confirmed, the presence of seagrass shoots significantly reduces the effectiveness of fish predation on a variety of epifaunal invertebrate and fish taxa, relative to their success on unvegetated substrates (Orth et al., 1984; Heck and Crowder, 1991; Heck et al., 2003).

What is perhaps more interesting, and challenging, is to untangle the interconnected roles that seagrass species' morphologies, biomass, surface areas, structural complexity, habitat patchiness, and

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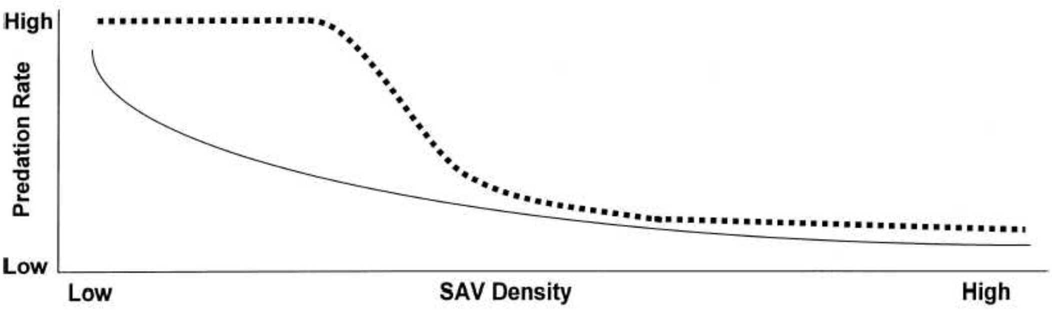

Fig. 1. Alternative models of the relationship between predation rate and submerged aquatic vegetation (SAV) density. Threshold model (------) originally proposed by Nelson (1979) and rejected by Nelson and Bonsdorff (1990) in favor of a monotonic decrease in predation rate with seagrass density (——). According to Bartholomew et al. (2000), the threshold model remains viable (see text).

fragmentation play in mediating predator success, along with the role that physical factors (e.g. waves and currents) may play in influencing the physical complexity of meadows over brief temporal scales. In addition, predator and prey morphologies and behaviors, including those that change during ontogeny, interact with these vegetative factors in ways that remain incompletely understood to determine the outcome of specific predator–prey encounters. For example, Orth and van Montfrans (2002) noted differential responses of blue crab (*Callinectes sapidus*) post-larvae and first instar crabs to predation by mummichogs (*Fundulus heteroclitus*) at different vegetation densities. Surprisingly, given the large number of species that occur within the seagrass canopy, there have been no studies conducted that examine how multiple species of predators and prey interact in the presence of vegetation. Below we note some seminal papers and summarize the current state of knowledge.

A. Direct Effects of Predation—Direct Effects of Seagrass Shoot Density, Biomass, and Surface Area

Nelson (1979) carried out one of the earliest experimental tests of the effects of seagrass density on the outcome of predator–prey encounters. He used different densities of an artificial substrate to mimic eelgrass (*Zostera marina*) leaves in laboratory mesocosms, with amphipods as prey and pinfish (*Lagodon rhomboides*) and grass shrimp (*Palaeomonetes vulgaris*) as predators. He found, as many others have since, that vegetation density reduced predation intensity, although not linearly, and he proposed the still controversial hypothesis (see below) that a threshold seagrass density might be required before any significant reduction in predator effectiveness would be realized. Heck and Thoman (1981), in both laboratory mesocosm and in field tethering experiments, obtained results that supported Nelson's (1979) conclusions regarding the non-linearity of density effects and the existence of thresholds. As Nelson and Bonsdorff (1990) correctly pointed out, however, earlier work that promoted the existence of thresholds was based on as few as four vegetation densities, and could not conclusively demonstrate whether a threshold existed. In their study, 11 different vegetation densities, again with artificial substrates, were used and they reported that the relationship between vegetation density and predation rate was linear, and that no threshold density was apparent (Nelson and Bonsdorff, 1990; Fig. 1). However, as Bartholomew et al. (2000) noted, predator satiation was likely evident in the low-density treatments in the Nelson and Bonsdorff (1990) study. This means that it was not possible to determine whether vegetation density or predator satiation were responsible for the results they obtained in their low and medium complexity treatments, because they used more prey than the predators could eat in the experimental time period. Thus, in the lowest complexity treatments, predators might have stopped feeding because they were satiated rather than because the different plant densities impeded their capture rate; and this could have biased the shape of the curve they obtained. In the only other similarly complex design of which we are aware, Gotceitas and Colgan (1989) conducted experiments with freshwater macrophytes at eight vegetation densities, using bluegill as prey and largemouth bass as predators, and found a threshold effect. The uncertainties in the results of Nelson and Bonsdorff's

(1990) experiments, together with the other evidence noted above, suggest that non-linear rates of prey capture at different vegetation densities may yet prove to be the case, although further testing is clearly still required.

With regard to the effect of seagrass surface area on predation rates, Stoner (1982) tested the protective abilities of seagrasses that differed in surface area/biomass ratios. He found that for single seagrass species, predation intensity declined with plant biomass and therefore plant surface area. However, in multi-species trials with similar biomasses, the seagrass species possessing the greatest amount of total surface area (*Halodule wrightii*) provided the least amount of protection. The likely reason for this unexpected result is that the spaces between the finely divided *H. wrightii* seagrass leaves and shoots did not match the size of the amphipod prey that were being attacked by visual fish predators. This was also the conclusion of Ryer (1988), who studied the vulnerability of different sized amphipods to fish predators in artificial eelgrass, and found that only when the spaces between leaves matched the size of prey did substantial refuge exist. And this is also the premise underlying the index recently proposed by Bartholomew et al. (2000) to quantify the degree of protection provided by seagrass leaves that might be generally applied across many types of complex habitats. The index is calculated as the ratio of the distance between structural elements (Sp) to predator width (Pr). The rationale is that spaces between structural components, such as seagrass shoots, that are smaller than a predator's width, should restrict predator movements and provide protection in predator–prey encounters. Although the index worked well in laboratory experiments with regularly placed structural elements (wooden dowels), it did not work as well in field trials in an intertidal salt marsh (*Spartina alterniflora*) habitat, nor did it give consistent results in mangrove prop roots when distances between roots were calculated for randomly, clumped, and uniform spacing patterns (Bell et al., 2003). This led Bell et al. (2003) to conclude that the index will only be useful for cross habitat comparisons when spatial arrangements of structural elements are similar, but that it is not a generally applicable means of comparing dissimilar structure across habitat types.

Also of interest, but rarely studied, is the behavior of prey as they use the structure provided by seagrasses to mitigate the impact of their predators. To date, the study by Main (1985, 1987) on the antipredatory behavior of the caridean shrimp *Tozeuma carolinense* in the presence of pinfish, *L. rhomboides*, remains one of the few studies to document how prey consistently avoid potential predators, in this case by moving around seagrass leaves and thereby maintaining an opaque barrier between themselves and pinfish.

An issue that, to our knowledge, remains unstudied, is how predators that forage from above the seagrass canopy might be influenced by seagrass density and/or biomass. For example, the height of the leaves and the degree to which they overlap each other could have significant impacts on the ability of down-looking predators to detect prey. In addition, the effects of wave-action could be important, as seagrass leaves sway back and forth with wave passage and alternately cover and uncover patches of the meadow. In such conditions, seagrass might provide less protection from predators foraging from above than from those foraging within the canopy. Because predators foraging from above the canopy will usually be larger, more mobile fishes, the logistics of conducting experiments at appropriate scales in the laboratory remains problematic.

With regard to studying the effect of seagrass on survival rates of infauna, Peterson and Heck (2001) recently reported that semi-infaunal mussels were preyed upon significantly less frequently when present in turtlegrass meadows than when living in unvegetated sand. Similar findings apply to studies of sub-lethal predation (e.g. siphon nipping), where Irlandi (1994; Irlandi and Mehlich, 1996) and others (Coen and Heck, 1991; Nakaoka, 2000) found reduced incidences of sub-lethal predation in seagrass meadows than on unvegetated substrates. These conclusions matched expectations and were generally similar to earlier investigations of the effects of seagrasses on predation of infaunal taxa (cf. Peterson and Quammen 1982; Blundon and Kennedy, 1982). To date, there are few studies of how infaunal species behave in the presence of predation risk, or even if they do, with the exception of siphonous bivalves, which respond by withdrawing their siphon in the presence of potential siphon nippers (Blundon and Kennedy, 1982; Irlandi and Peterson, 1991; Nakaoka, 2000). How infaunal taxa detect and avoid the different types of predators that attempt to prey upon them remain questions for future research.

Temporal differences in predation rates on seasonal and annual scales have been quantified by field tethering experiments (e.g. Heck and Wilson, 1987; Heck et al., 2001) and, not surprisingly, the ability of vegetation to provide protection from predators was usually observed, as were substantial seasonal and annual differences in predation rate. Less well-studied are diurnal differences in predation rate in vegetated habitats, and the few studies that exist did not find identical patterns. For example, using chronographic tethering techniques, Peterson et al. (2001) found no significant differences in predation rates on shrimp and crabs between light and dark periods in eelgrass beds in the Damariscotta River estuary (Maine, USA), while they found significantly higher rates of daytime predation in St. Joseph Bay turtlegrass beds (Florida, USA). Different numbers of night active predators between the two areas were suggested as an explanation for these location differences. In Newfoundland (Canada), Lineham et al. (2001) used tethers to measure predation rates on small cod in eelgrass and nearby unvegetated substrates during day, dusk, and night. They found that predation rates were greatest during the day and dusk, and lower at night, but overall rates were lower in vegetation than on unvegetated substrates.

Because different predators forage at different times of day, depending on the mode of foraging, one could expect day vs. night predation rates to fluctuate seasonally and annually as the composition of predators changes. Overall, while the number of studies on the effect of time of day on predation rates in seagrass meadows is very small, the few studies that exist are consistent with what one might expect, given a knowledge of the predator assemblages in any given area.

On balance, the existing literature shows that, although there are differences in details, seagrass presence is almost always negatively related to predation effectiveness, and that increasing seagrass abundance is usually associated with decreasing predator effectiveness. The only exceptions we know are those of James and Heck (1994). In that study, the foraging rate of the seahorse (*Hippocampus erectus*), an ambush predator, was not significantly negatively influenced by increasing density of artificial seagrass. Although it seems likely that studies with other ambush predators would produce similar results, there are no additional data to evaluate this proposition, and more studies would be welcome.

All previous studies that have investigated the effects of vegetation density on predation success have been done in a similar manner, and one that calls into question much of what has become the conventional wisdom. As far as we know, the experimental design in all previous laboratory experiments has been to test the effects of a constant number of predators on a constant number of prey items at different levels of vegetation density. However, as shown repeatedly in sampling studies, both the numbers of prey and predators almost always increase with increasing vegetation density (Orth et al., 1984; Edgar, 1990; Edgar and Shaw, 1995; Boström and Bonsdorff, 1997; Jenkins et al., 1997; Wyda et al., 2002). Thus, the results from laboratory experiments done to date, in which predator and prey densities were kept constant as vegetation density was increased, appear to have poorly mirrored reality and resulted in an incomplete understanding of how seagrass influences predator–prey interactions in nature.

In aquarium experiments where pinfish (*L. rhomboides*) were used as predators and grass shrimp (*Palaemonetes pugio*) as prey, Mattila and Heck (in review) studied predation effects on an unvegetated substrate and at three different densities (400, 2,000, and 4,000 leaves m^{-2}) of artificial seagrass (a mimic of turtlegrass, *Thalassia testudinum*). Their results showed that seagrass provided significantly more shelter than unvegetated substrate, but no significant differences were found among different seagrass densities (Fig. 2). These results conflict with those of most previous experiments that tested the sheltering role of seagrass, where increasing leaf density was associated with increased prey survival. However, Mattila and Heck's (in review) experimental design differed from all previous experiments in that both the numbers of prey and predators were increased with increasing seagrass density, thereby mimicking what is observed in nature, whereas previous experiments were conducted with constant numbers of prey and predators at differing densities of seagrass. These results indicate that it is not safe to assume that increasing vegetation density will consistently lead to proportionally higher prey survival.

B. Indirect Effects on Growth and Food Webs

A recent meta-analysis (Heck et al., 2003) found, as expected, that growth of macrofaunal species was significantly greater in seagrass meadows than on unvegetated substrates, although the number of studies in the analyses was small. However, an issue addressed infrequently over the years is how seagrass density affects the growth of animals. If prey capture

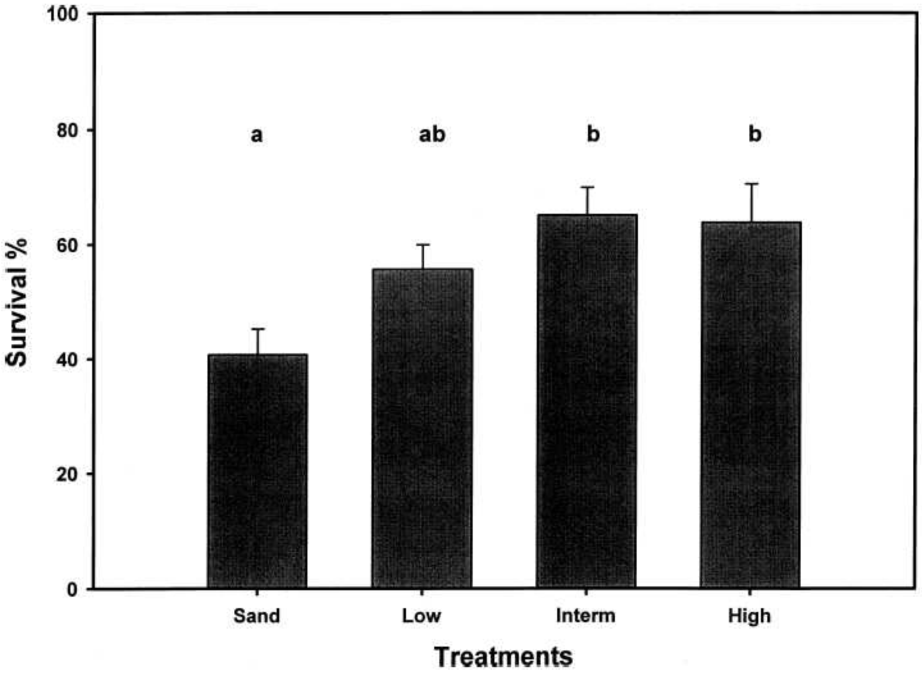

Fig. 2. Predation rate as a function of seagrass density when predator and prey densities increase proportionally as seagrass density increases. Note difference between these data and those in Fig. 1 Different letters indicate significant differences ($p < .05$), as detected by 1-way ANOVA (after Mattila and Heck, in review).

rate were reduced in dense vegetation, it would follow that growth rates of predators should also be reduced as seagrass leaf density increases. A great deal of work has been done to assess the effects of seagrasses on the growth of suspension feeding bivalves (hard clams *Mercenaria mercenaria*), but results are equivocal—growth is sometimes increased, decreased, or remains unaffected by the presence of different densities of seagrasses (see summary in Heck et al., 2002). In an unexpected result, Bologna and Heck (1999) found that although bay scallops were preyed upon at higher rates in sparse seagrass at the edge of a turtlegrass meadow than in adjacent sand patches or the interior of the meadow, scallops grew faster at the edge than elsewhere. This appears to be a simple case of scallops trading off lower probabilities of survival for increased growth rates at the edges of seagrass beds. However, the pattern was only recognized because distinct portions of the seagrass beds (i.e. edges and interiors) were studied separately, something not often done, as treatments are usually only described as either 'vegetated' or 'unvegetated'. This is the usual case with studies of fishes, which typically compare growth rates of juvenile fishes between different habitat types, such as marshes or seagrass meadows, and not within seagrass meadows of varying shoot density (e.g. Phelan et al., 2000; Stunz et al., 2002).

However, a study by Spitzer et al. (2000) found that growth of young-of-the-year pinfish (*L. rhomboides*) in high density turtlegrass was consistently less than in low or intermediate density turtlegrass, which is consistent with predictions made long ago that growth should be reduced at high shoot densities (Fig. 3; Heck and Orth, 1980). However, the conclusions of Spitzer et al. (2000) are subject to the caveat noted above; namely, that densities of pinfish were kept constant among the different densities of seagrass and not allowed to increase with increasing shoot densities. Findings from experimental work in freshwater macrophyte beds also appear to be consistent with this model. Gotceitas (1990a,b) found juvenile bluegills (*Lepomis macrochirus*) preferred patches of artificial vegetation with lowest stem densities in maximizing foraging rate in the absence of predators. However, with predators (bass, *Micropterus salmoides*) present, bluegills traded foraging success for safety in higher density vegetation.

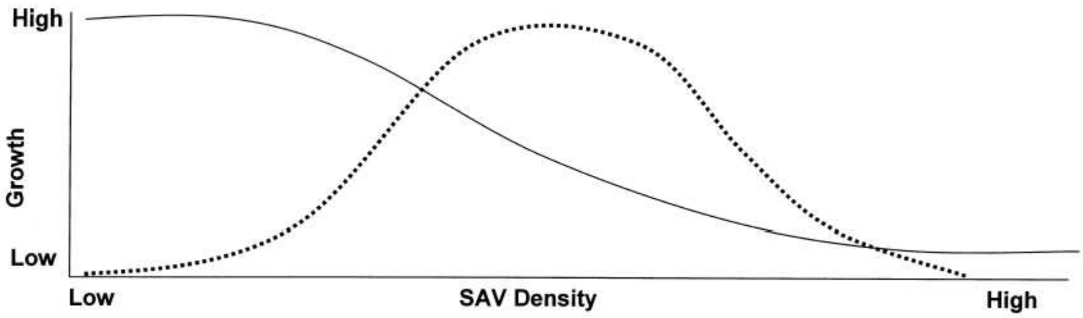

Fig. 3. Models of small fish growth as a function of SAV density proposed by Crowder and Cooper (1979, ——) vs. that of Heck and Orth (1980, ...). According to Spitzer et al. (2000), the Heck and Orth (1980) model is a better descriptor of small fish growth.

One of the more challenging issues ecologists have dealt with recently is the relative importance of 'top-down' and 'bottom-up' control of ecosystem structure and function. The prevailing view regarding the effects of nutrient enrichment on seagrasses has been that increasing nutrient supplies lead to the overgrowth of seagrasses by fast-growing algae and the eventual disappearance of seagrasses from eutrophic systems, i.e. 'bottom-up' control (Duarte, 1995; Bricker et al., 1999; Howarth et al., 2000; NAS, 2000; Hauxwell et al., 2001). This is the explanation most often proposed to account for the loss of seagrasses in North America (Orth and Moore, 1983; Neundorfer and Kemp, 1993; Short et al., 1995; Tomasko et al., 1996), Europe (Giesen et al., 1990; Den Hartog, 1994), and Australia (Cambridge and McComb, 1984; Shepherd et al., 1989). However, as noted previously by Heck et al. (2000), every experimental study that included mesograzers (i.e. small crustacean, gastropod, or fish that consume algae) in their design, found that grazing effects explained more of the variance in their data set than those of nutrient enrichment (Neckles et al., 1993; Williams and Ruckelshaus, 1993; Phillippart, 1995; see also Valentine and Duffy, Chapter 20).

More recently, Lin et al. (1996) concluded that epiphyte biomass was not a good indicator of nutrient loading in shallow coastal lagoons, and that epiphyte responses to nutrient enrichment were surprisingly complex. Of primary importance, they concluded, were system level faunal interactions that produced results that differed from previous studies that did not include complex plant–animal interactions. In experiments in turtlegrass (*Thalassia testudinum*) meadows, Heck et al. (2000) also found few significant nutrient effects on epiphyte biomass or on seagrass aboveground biomass, production or leaf morphology. In contrast, manipulation of pinfish densities resulted in significant effects on mesograzer density, epiphyte biomass and the production, leaf length, and shoot density of *T. testudinum*. The results from these studies clearly showed that when mesograzers were present, the stimulatory effects of increased nutrient loading on epiphyte abundance were greatly reduced. Thus, mesograzers usually controlled the abundance of epiphytes, even in enriched conditions, a result clearly inconsistent with the paradigm of nutrient-enrichment based seagrass decline summarized by Duarte (1995) and in a number of other authors (Bricker et al., 1999; Howarth et al., 2000; NAS, 2000; Hauxwell et al., 2001). However, this is consistent with the hypothesis that cascading trophic effects, like those caused by the effects of overharvesting large predators (Fig. 4; see also Jackson et al., 2001) can have important consequences for the flora and fauna of seagrass meadows (Heck et al., 2000; Williams and Heck, 2001), via 'top-down' control.

Freshwater submerged aquatic vegetation (SAV) research in the United Kingdom has gone through a transformation that seems to be similar to what we suggest for seagrasses. In British lakes, nutrients were first thought to be the driving force leading to the demise of rooted macrophytes (see Phillips et al., 1978). However, Jones and Sayer (2003) suggest that the major determinant of shallow water plant structure is actually fish predation on invertebrates, which through a trophic cascade indirectly influences the biomass of periphyton and, thus, rooted macrophytes.

While nutrient enrichment certainly is an extremely important issue in numerous estuarine and coastal areas throughout the world (see, e.g. Walker et al., Chapter 23), because of its association with phytoplankton and macroalgal blooms, food web

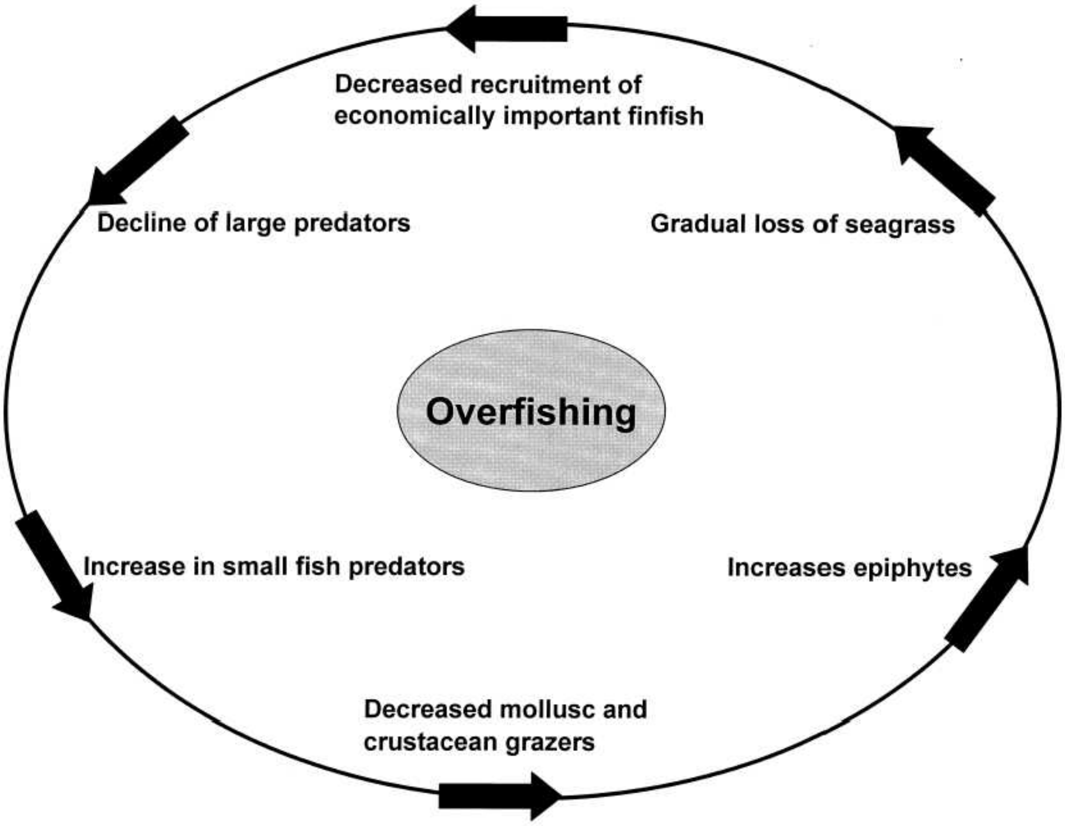

Fig. 4. Mechanism by which overfishing can initiate cascading trophic effects that result in algal overgrowth of seagrasses and eventual seagrass disappearance (after Williams and Heck, 2001).

interactions should not be overlooked in future studies of eutrophication. The hypothesis that top-down control in seagrass meadows is common, requires much further testing, but if true, it has practical implications (e.g. reducing nutrient inputs to coastal waters may not bring about full seagrass recovery if epiphyte grazers are artificially low in abundance), as well as fundamental importance for understanding the relative role of top-down and bottom-up effects in various types of seagrass meadows.

C. Predation at the Landscape Level

As noted above, the majority of studies conducted on predator–prey dynamics in seagrass meadows have focused on the influence of various aspects of structural complexity, notably shoot density, biomass, or leaf surface area, on prey survival. This level of complexity may be most meaningful for sessile animals, either infaunal or epifaunal, as well as small, mobile fauna whose foraging range may be at the scale of meters. However, larger, more mobile predators that forage over kilometers may respond less to this level of complexity but more to landscape features such as patchiness or fragmentation, size of bed and proximity and connectivity to other habitats that could serve as additional foraging areas (see Bell et al. Chapter 26).

Recent studies have shown how important these issues can be. For example, Irlandi et al. (1995) found predation rates on bay scallops (*Argopecten irradians*) to be higher in very patchy seagrass beds than in less patchy or continuous beds. Plant characteristics normally associated with prey survival, i.e. shoot density, biomass, and blade length, were not significantly different among beds of different spatial configurations, and thus could be ruled out as influences on their results. Hovel and Lipcius (2002) found that eelgrass (*Zostera marina*) patch size and complexity (shoot density) both contributed to blue crab (*Callinectes sapidus*) survival, but the influence varied temporally. Irlandi and Crawford

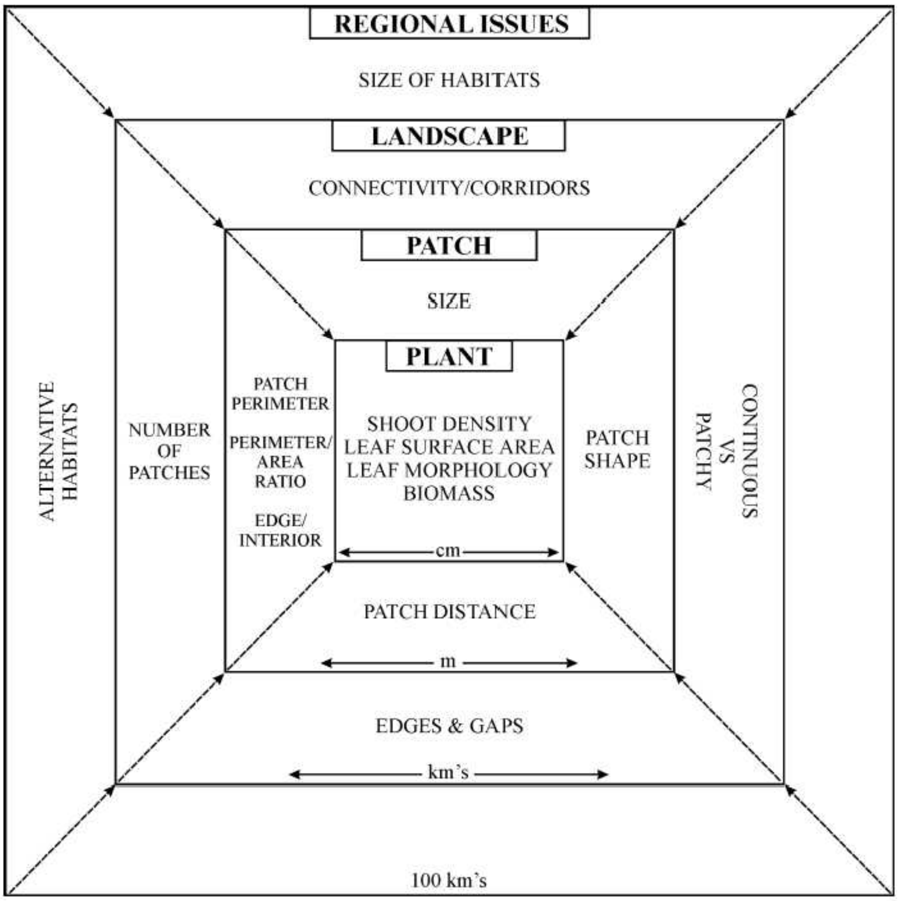

Fig. 5. Conceptual model of how predator–prey interactions in seagrass beds may vary at different spatial scales, from small (e.g. shoot density, leaf surface area), to larger (e.g. seagrass bed size, shape and degree of patchiness or fragmentation), to landscape scales and to even larger regional scales (e.g. between estuaries and rivers).

(1997) found greater movements and greater growth of pinfish (*Lagodon rhomboides*) when marsh and subtidal seagrass were juxtaposed than when unvegetated habitat occurred next to marsh. Micheli and Peterson (1999) found that seagrass corridors between marsh and oyster reefs may have contributed to increased mortality of bivalves.

While the above studies address issues that go beyond the relatively simplistic complexity issues of shoot density or leaf surface area, they only approach problems on scales up to a few hundred meters. To date, there are no studies that address predation on scales of km to 10s of km or more, although there are many species that have very large foraging ranges and when moving in schools have the potential to markedly influence prey populations. Species such as red drum (*Sciaenops ocellatus*), spotted sea trout (*Cynoscion nebulosus*) and various species of sharks, for example, all have been documented to forage in seagrass meadows (e.g. Orth and Heck, 1980; Heithaus et al., 2002) yet their impacts remain relatively unknown. There is significant anecdotal evidence that abundances of these large species vary greatly both temporally and spatially, and many of these species migrate 100s of km in a single season and can influence disjunct prey populations in ways that remain uninvestigated.

In Fig. 5, we summarize our thoughts on how predator–prey interactions may differ at various spatial scales. At the smallest scale (cm), plant characteristics should be more important for smaller, less mobile predators, while predators capable of foraging over large areas (km to 100 of km) should be influenced more by landscape features such as size, shape and number of patches, proximity to alternative foraging areas (e.g. marshes, mangroves or coral reefs) and connectivity of patches and these other habitats (see Bell et al., Chapter 26 for more discussion of the effects of scale).

III. Effects of Seagrass on Predator–Prey Interactions in Evolutionary Time

As a preamble to this section, we note that the abundance of many wide-ranging predators is clearly much lower than what it was in earlier centuries (Jackson et al., 2001; see also Valetine and Duffy, Chapter 20), and that ecologists have been studying the effects of predation in conditions that are different from those in which predator–prey relationships evolved (Dayton et al., 1998; Jackson et al., 2001; see also Valentine and Duffy, Chapter 20). With this caveat in mind, we consider the major hypotheses concerning the evolution of predator–prey interactions among seagrass-associated animals.

We begin by noting that there are a number of well-camouflaged invertebrates and small fishes that inhabit seagrass meadows. Familiar examples include many shrimps and crabs, pipe fishes and seahorses, and many guidebooks include striking photographs of how effective the camouflage of certain species appears to be. The usual interpretation of such cryptic appearances is that they have evolved over many thousands of generations (i.e. in evolutionary time) as a means of reducing the effectiveness of predators. However, there have been few attempts to test the effect of removing or changing the structures or colors suspected to provide the camouflage on survival rates. A potentially confounding factor is that, if the protection is provided by living organisms such as algae or invertebrates, chemical defenses, instead of camouflage, may be the primary means by which refuge from predation is obtained (Stachowicz and Hay, 2000). Thus, carefully designed experiments capable of distinguishing between the alternatives of camouflage or chemical defense are required to evaluate additional suspected cases of camouflaging behavior involving living organisms.

Several types of behaviors suggest that predation has affected seagrass-associated animals in important ways. The work of Main (1985, 1987) described above, showed how stereotyped adult behavior could evolve in response to the threat of predation. Larval behavior can also be affected, as the preference for seagrass shoots by settling blue crab (*Callinectes sapidus*) megalopae clearly demonstrates (Forward et al., 1996). This estuarine crab preferentially settles from the plankton into seagrass meadows [and can even be induced to settle by the extract of seagrass shoots (Forward et al., 1996)], where predation rates on juveniles are significantly lower than in adjacent unvegetated substrates (Heck et al., 2001; Orth and van Montfrans, 2002). Because there are only a few other investigations of these types, there remains much to learn about relationships between predation risk and prey behavior.

There is also evidence that predation rates on crabs in seagrass meadows vary latitudinally, with higher predation rates in tropical than temperate meadows in the western Atlantic Ocean (Heck and Wilson, 1987; Heck and Coen, 1995). This is consistent with other demonstrations of higher intensity of predation in tropical intertidal zones (Bertness et al., 1981; Menge and Lubchenko, 1981), as well as Vermeij's (1987) well known thesis that higher rates of predation by durophages (shell-crushing predators) in tropical regions have led to the evolution of better armored and predator-resistant prey in low latitudes. With only a few studies carried out so far, here too there are many opportunities for more and better testing of the hypotheses that seagrass-associated animals will be better armored and more resistant to crushing predators than temperate analogues. Similar comparisons of whether latitudinal patterns in chemical defenses exist in seagrass inhabitants would also be interesting.

The protection provided by seagrasses has likely led to many indirect effects on the suite of species currently associated with seagrass meadows. While very few well-understood examples exist, we expect that there are many complex relationships remaining to be discovered. The few cases that have been investigated all involve suspension-feeding bivalves that survive at enhanced rates in seagrass meadows than elsewhere. Reusch et al. (1994) and Reusch and Williams (1998) have shown that native mussels may enhance eelgrass growth by fertilizing pore waters, but also that an introduced mussel species can compete successfully with seagrasses for space belowground. Peterson and Heck (2001) demonstrated that not only do mussels enhance the growth of turtle grass by fertilizing pore waters, but they also support additional numbers of grazers that more effectively prevent epiphytic algae from growing on seagrass leaves. Thus, it appears that both mussels and turtle grass experience elevated survival or growth when co-occurring than when growing alone.

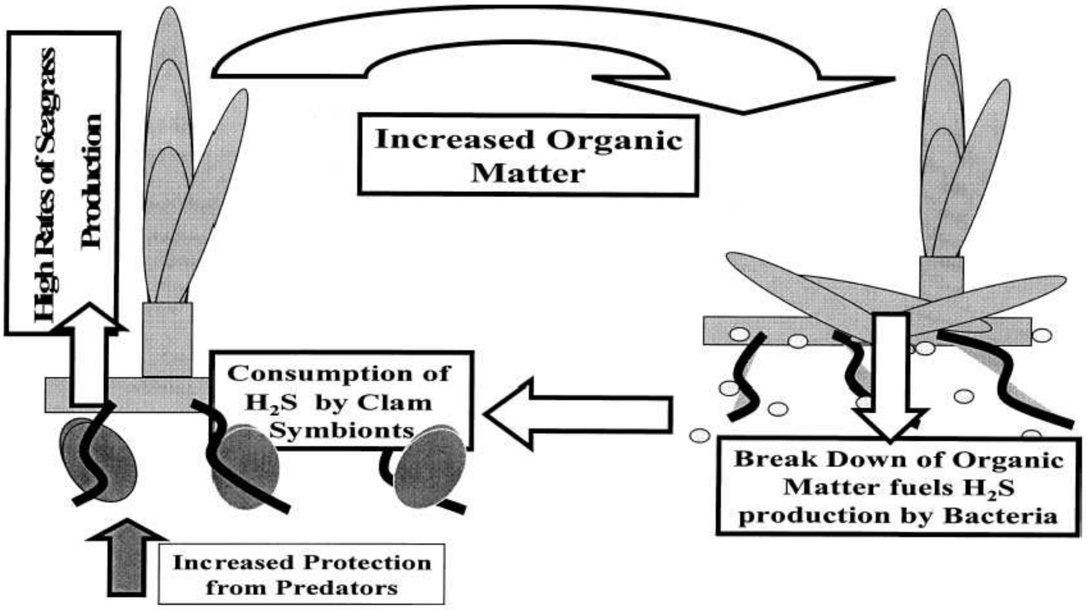

Fig. 6. Model of positive interactions between seagrasses and lucinid bivalves containing sulfur-reducing bacteria. In this scenario, bivalves benefit from reduced predation rates when inhabiting the seagrass rhizosphere, while seagrasses benefit from lowered sulfide concentrations owing to the chemosynthetic activities of the bacteria present in the lucinids.

Another possible example of mutualism between seagrasses and their animal associates involves infaunal bivalves in the family Lucinidae and their long history of association with seagrasses. Lucinids have been associated with seagrass meadows since the Cretaceous (Bretsky, 1978), where they were often extraordinarily abundant (Stanley, 1970; Jackson, 1973). Lucinids in seagrass meadows harbor chemosynthetic sulfur-reducing bacteria, which provide the bivalves with nutrition in the same way that the better known mussel-chemosynthetic bacterial associations operate at hydrothermal vents (Fisher, 1990; Barnes and Hickman, 1999). This means that the bacteria within the shells of lucinids reduce hydrogen sulfide concentrations in the organic-rich seagrass sediments. Since sulfide is toxic to seagrass roots and rhizomes (Carlson et al., 1994), lucinids and their symbionts can reduce stress to seagrass belowground tissues. Just as other bivalves are provided protection from predators by seagrass roots and rhizomes, so too we expect lucinids to receive protection (Fig. 6). This scenario indicates the types of complex, indirect interactions that might be due to protection afforded to seagrass-associated organisms, which we would expect to find more commonly in high predation intensity tropical seagrass meadows.

IV. Summary

The ability of seagrass leaves, roots and rhizomes to reduce the rate of predation on associated animals is well studied, and is one of the tenets of the seagrass ‘nursery role hypothesis’. While the major conclusions concerning the effects of seagrasses on the outcome of predator–prey interactions remain unchallenged, some older issues remain unresolved and new issues have arisen. For example, there is continuing uncertainty about the shape of the curve describing the negative effects of seagrass structure on prey capture rate (i.e. are there thresholds or not?). And not all animals grow faster in seagrass than in unvegetated areas, a finding that was unexpected and deserving of further study. In addition, there is the recent demonstration that predation pressure remained unchanged when the ratios between predators, prey and seagrass surface area were kept constant. This conflicts with all previous results in which increasing leaf density was associated with increased prey survival. It seems attributable to allowing numbers of both prey and predators to increase as seagrass density increased (mimicking what is actually observed in nature), while previous experiments used constant numbers of prey and predators at differing densities of seagrass. Other areas that remain understudied and offer great promise include analyses of predator and prey behavior during encounters, further assessment of the relative effects of top-down control of seagrass ecosystem structure and function, and increased understanding of positive interactions between seagrasses and their animal associates. Landscape level and regional issues such as gap dynamics, habitat connectivity (corridors), alternative habitats and habitat fragmentation should also figure prominently in future studies, especially with larger predators that forage over large areas. In addition, there is a need to evaluate the influence of waves and currents in altering the structure and complexity of the meadow, and whether this affects relationships between prey and predators. Lastly, efforts by conservationists to restore large predators to their prior abundances could produce many unanticipated changes in marine ecosystems (Peterson and Lipcius, 2003), and the increasing number of marine protected areas (MPAs) provides unparalleled opportunities for testing the direct and indirect effects of large predator abundance on the faunal and floral components of seagrass meadows (cf. Valentine and Heck, in press).

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Chapter 23

Decline and Recovery of Seagrass Ecosystems—The Dynamics of Change

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I. Introduction

The distribution of seagrass beds has often been described in the literature as if these communities were naturally static components of coastal ecosystems (Larkum, 1977; McRoy and McMillan, 1977; Orth and Moore, 1983; Kirkman and Kuo, 1990), disturbed only by human influences. A paradigm of seagrass bed stability, developed for large bed-forming seagrasses such as *Posidonia* as in the Mediterranean Sea (Boudouresque et al., 1980), and the western and southern coasts of Australia (Larkum, 1976; Larkum and West, 1983; Kirkman, 1978), suggested that sea level had been stable for the last 5–8,000 years and assumed that these large monospecific seagrass beds were static for that period.

Immense variations have been shown in detailed studies of such beds, on a seasonal and spatial basis (e.g. Duarte et al., 1994; Alcoverro et al., 1995; Duarte et al., 2003). Change is a naturally-occurring process, which takes place in the absence of human influence (Patriquin, 1975; Hottinger and Vischer, 1983; Clarke and Kirkman, 1989; Marba and Duarte, 1995; Marba and Duarte, 1998). There have also been massive declines in seagrass due to anthropogenic effects (Orth and Moore, 1983; Walker and McComb, 1992; Short and Wyllie-Echeverria, 1996), raising the possibility that such losses may be irreversible. Recent research findings suggest this is not the case (Kendrick et al., 1999, 2002).

This chapter will detail aspects of more recent research demonstrating changes, both negative and positive, in seagrass distributions, as revealed by mapping and other detailed investigations. The extent of decline dominates the literature, but an increasing number of studies record the dynamic nature of seagrass meadows (Williams, 1988; Kendrick et al., 1999, 2000, 2002; Cambridge et al., 2000, 2002; Durako et al., 2002). The rates of decline and recovery will be compared. The evidence for large-scale recovery of seagrass beds, based on mapping projects, will then be described. A case study will be presented that compares and contrasts two regions on the Western Australian coast: Cockburn Sound, where seagrass loss has been dramatic and is continuing; and Success and Parmelia Banks where loss and recovery are in dynamic equilibrium or seagrasses are expanding into unvegetated sand habitats. Comparisons and contrasts in findings in Florida Bay (USA) will be explored. We will conclude by suggesting a way in which management of seagrass landscapes can be made proactive to match their dynamic nature.

II. Changes in Seagrass Distributions

Many seagrass studies have been made at scales less than a 1 m^2 quadrat or a 10-m transect, over time scales of 1–2 years (e.g. Hillman et al., 1989; McMahon and Walker, 1997). On the other hand, seagrass losses have been documented over tens of square kilometres (Orth and Moore, 1983;

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Cambridge and McComb, 1984; Walker and McComb, 1992; Marba et al., 1996; Short and Wyllie-Echeverria, 1996; Kendrick et al., 2002). The processes that influence the presence and persistence of seagrasses operate at scales somewhere between these extremes. They consist of local destruction of beds by exceptional storms that occur every 30–50 years, affecting spatial scales of 5–10 km; accumulations of sand sheets that influence 100 m to 2 km, which can provide entirely new habitats over periods of 5–20 years; or the frequent formation of gaps (1–100 m) in existing beds during winter storms. Large-scale studies provide information on net rate of change, but provide no insight into the controlling mechanisms, making prediction difficult. In turn, process studies at small scales (shoot) cannot be safely extrapolated to the landscape scale (Vidondo et al., 1997; Kendrick et al., 1999), as both models and field studies have shown that properties of the landscape emerge at intermediate scales to create seagrass patches, which in turn render extrapolation from small- to large-scale processes uncertain. This subject is discussed in many other places in this book, especially, Duarte et al. Chapter 11 and Bell et al., Chapter 26.

The seagrass literature also contains contradictory statements regarding recovery of seagrasses from disturbance and the roles of recruitment from seedlings and clonal growth. Recovery of seagrasses from disturbance is reported to be slow, and take many decades to centuries (Kirkman, 1985; Clarke and Kirkman, 1989; Kirkman and Kuo, 1990; Meehan and West, 2000). Recovery is reported to be primarily from clonal growth (lateral growth of rhizomes) as recruiting seedlings do not survive in any great number (Kirkman, 1998; but see Orth et al., Chapter 5). In contrast, however, Kendrick et al. (1999, 2000) have documented landscape-scale increases in seagrass cover over 2–3 decades and these increases are not solely due to clonal growth, suggesting recruitment from seedlings may also play a role in colonization and recovery. Marbà and Duarte (1999) have demonstrated that growth rates of seagrass rhizomes measured at the scale of shoots (cm) may not extrapolate to the growth dynamics of seagrass patches or meadows (see also Vidondo et al., 1998). Patch growth of *Cymodocea nodosa* in the Mediterranean accelerated with increased patch size and age which was not due to an increase in rhizome spreading rates (Marbà and Duarte, 1995; Vidondo et al., 1997). Relatively high rates of flowering have been found in temperate Australian seagrasses in general (Marba and Walker, 1999) and *Posidonia* spp. specifically (Waycott et al., 1997; Walker et al., 2001; Campey et al., 2002). Seedling survival rates of *Posidonia* species are also relatively high (1–10%: Kuo and Kirkman, 1996; Gobert et al., Chapter 17). Seagrass recruitment from seed and clonal growth can and does occur. The question remains: does the rate of recruitment match the rates of seagrass decline? In this review, we assemble information to allow comparisons between rates of recruitment and rates of decline.

III. Loss of Seagrass Beds

Mechanisms of seagrass decline are covered in detail in Kenworthy et al., Chapter 25. The documented loss of seagrass from direct and indirect human impacts amounts to 33,000 km^2 or 18% of the documented seagrass area, over the last two decades (Green and Short, 2003), based on an extrapolation of known losses (Short and Wyllie-Echeverria, 1996). Such declines have been widespread in shallow coastal seas and estuaries (see reviews by Walker and McComb, 1992; Short and Wyllie-Echeverria, 1996 and Chapter 25). Loss of seagrass is usually correlated with decreases in light intensity and/or increases in sedimentation, or direct physical removal by coastal engineering. Recovery of seagrass is by recruitment and clonal expansion.

A. Seagrass Dynamics and Mapping Studies

Most large-scale studies of the distribution of seagrasses have reported losses, but generally those studies were commissioned because of an environmental disaster, or because an issue had already been reported (Table 1). In these studies the researcher has documented the scale of loss, funded by and for management agencies. These studies are well summarized in recent research articles and reviews (Walker and McComb, 1992; Marbà et al., 1996; Short and Wyllie-Echeverria, 1996; Kendrick et al., 2000). Large-scale recovery of seagrasses on unvegetated intertidal and subtidal environments have been increasingly reported from mapping studies (Table 2). These increases in seagrass cover receive less recognition than they should. They infer the spatial scales and temporal rates of recovery over a range of seagrass species, from fast growing tropical species (e.g. *Halodule* species—Robbins, 1997; Robbins and Bell, 2000) to slow growing temperate

Table 1. Causes and scales (spatial and temporal) of natural declines and recovery. G, gain; L, loss.

System location and species	Extent of loss/gain	Cause	References
Success Bank, *Amphibolis griffithii, Posidonia coriacea*	G—17.6 ha year^{-1} in the West L—1.2 ha year^{-1} in the East	Natural expansion by recruitment and infilling	Kendrick et al. (1999, 2001)
Parmelia Bank, Western Australia	L—1.2 ha year^{-1}	Natural changes in patches	
Two People Bay, WA	L—40% of 4 km^2 bay, 1984 G—20% of 4 km^2 bay 1984–2002	Storm removal Natural expansion of meadows by recruitment and infilling	Kendrick et al. (submitted)
Denmark, *Zostera marina*	G—5 × 10^{-3} patches ha^{-1} year^{-1}	Patch formation	Olesen and Sand-Jensen (1994)
Mediterranean, *Cymodocea nodosa*	G—5 × 10^{-3} patches m^{-2} year^{-1}	Patch formation	Duarte and Sand-Jensen (1990)
Mediterranean, *Posidonia oceanica*	G—3 × 10^{-4} patches ha^{-1} year^{-1}	Patch formation into bomb blastings	Meinesz and Lefèvre (1984)
Great Bay, NH, USA, *Zostera marina*	L—700 ha between 1986–1989 G—630 ha in 1990	Wasting disease Recovery from seeds	Short et al. (1987) Short (personal communication, 2003)
Western Port Bay, Victoria Australia	L—16,200 ha year^{-1}	Exposure, desiccation, fine muds settling on leaf blades	Bulthuis et al. (1984), Seddon et al. (2000)

species (e.g. *Posidonia* spp.—Kendrick et al., 2000). Mapping exercises have generally used coarse grains (>1 m^2 photograph resolution and >25 m^2 mapping resolutions) and extremely large extents (Table 2). Linking the recovery of seagrass reported from mapping exercises to seedling recruitment and rhizome growth characteristics of individual species is difficult and rarely attempted (for exceptions see Kendrick et al., 1999 and Robbins and Bell, 2000).

In sub-tropical and tropical seagrasses, the speed of growth of some species results in seagrass distributions changing annually, or over a few years (Robbins, 1997; Robbins and Bell, 2000). Increases mostly occurred on the margins of existing patches for *Halodule wrightii* and *Thalassia testudinum* in Florida (Robbins and Bell, 2000). Robbins (1997) reported that new patches of *Halodule wrightii* arose between 1988 and 1992 in Tampa Bay, Florida and inferred these patches were potential seedling recruitment events, but also stated that interpretation was limited by the 2.5 ha minimum mapping unit employed.

In species of Cymodoceaceae, annual vegetative spread can also be rapid. Vidondo et al. (1998) reported rapid patch growth in *Cymodocea nodosa* in Alfacs Bay, Spain over 5 years. The growth of patches was faster than linear growth rates of individual shoots. Similarly, Kendrick et al. (1999) found 4 ha landscape units of *Amphibolis griffithii* over 23 years infilled faster than radial spread of rhizomes, as they demonstrated in a model based on linear rhizome growth rates in that species. They inferred that seedling recruitment may also play a role in patch creation and landscape infilling, and went on to demonstrate that over 400 ha expansion of seagrasses between 1965 and 1995 on Success, and Parmelia Banks was predominantly in patches and meadows of *Amphibolis griffithii* (Kendrick et al., 2000).

In slower-growing species of the temperate genus *Posidonia*, patch spread has been measured only once in *Posidonia australis* (Cambridge et al., 2002). Partly, this relates to slow linear rhizome growth rates (for example, *Posidonia oceanica* 30 cm year^{-1} Duarte, 1995; *Posidonia sinuosa* 7.2–18 cm year^{-1}, Marbà and Walker, 1999). Yet patch extension and landscape infilling have been reported at 10 m^2 to ha mapped scales. The endemic Australian species *Posidonia coriacea*, forms clumps and patches rather than meadows because of its predominantly vertical rhizome growth and branching, and is responsible for >120 ha of seagrass expansion between 1965 and 1995 on Success and Parmelia Banks (Kendrick et al., 2000). Meehan and West (2000) clearly demonstrated regrowth of the temperate Australian species, *Posidonia australis,* into sand patches within a meadow created by explosives in Jervis Bay over the past 50 years. They also predicted that another decade would be required before the sand patches were fully colonised. In mooring areas at Rottnest Island, Western Australia, Hastings et al. (1995) observed that recovery of *P. sinuosa* into

Table 2. Survey of seagrass mapping exercises from Australia, USA and Europe, published between 1990 and 2002, showing recovery (expansion) of seagrasses vs. losses.

Authors	Location	Remote sensing type	Spatial extent	Method of mapping	Comments
Recovery (expansion)					
Robbins (1997)	Tampa Bay, Florida, USA	Colour aerial photographs	103,082 ha	Photos used from 1988, 1990, and 1992 minimum mapping unit of 2.5 ha 15–30 m error in boundaries mapping categories 95–99% accurate from ground truthing.	Mean depth of water = 3.7 m Seagrass aerial extent in: 1988 = 9,258 ha 1990 = 10,450 ha 1992 = 10,759 ha noted 2.5 ha min mapping unit was too large for patchy nature of change in seagrasses.
Ward et al. (1997)	Izembek Lagoon, Alaska	1978 Landsat and 1987 B/W aerial photograph 1995 ground survey	33,000 ha		*Zostera marina* stable between 1978 and 1995 covering 15,00–16,000 ha Changes were 1978–1987 +6% 1987–1995 +1%.
Jaubert et al. (1999)	Bay of Menton, France	Colour aerial photographs, CASI aerial scanner—geolocated	910 ha	Mapped to a maximum depth of 17 m. Aerial photographs could not map <10% cover.	Change in seagrass cover over 10 year period 1988–1997. No beds of *Posidonia oceanica* have been displaced by *Caulerpa taxifolia*.
Kendrick et al. (2000)	Success and Parmelia Banks, West. Australia	Colour and B/W aerial photographs rectified and mosaicked	3,974 ha	Control rules were: isolated patches less than 30 m^2 not mapped; isolated patches 30–100 m^2 mapped as separate meadows when distance between patches was greater than diameter of patches; seagrass patches 30–100 m^2 were mapped together when they are not isolated by sand > diameter of seagrass patch; seagrass patches >100 m^2 were mapped as separate meadows. Spatial errors varied from 2.5 to 13.9 m between years mapped.	Changes in area of seagrass coverage were recorded between 1965, 1972, 1982, and 1995 21% increase in seagrass cover on Success Bank. On Parmelia Bank % cover of seagrasses has remained constant at approximately 45% Seagrasses responsible for gains are *Amphibolis griffithii* and *Posidonia coriacea*.
Robbins and Bell (2000)	Tampa Bay, Florida, USA	Colour aerial photographs	5 ha	Spatial accuracy of ±0.5 m.	Changes between spring and autumn 1994, 1995. Overall increase in seagrass cover of 14%. Majority of change occurred along the margins of existing patches. Comparison between *Thalassia testudinum* and *Halodule wrightii*.
Meehan and West (2000)	Jervis Bay, New South Wales, Australia	Colour and B/W aerial photographs	2,000 ha	Error term estimated at 15%; pixel size ranged from 0.63–0.71 m.	Historical aerial photographs 1972,1981,1993, 1997; decrease in the areas of blast holes 21 ± 2 cm. Full recovery estimated at 2034–2071.

(*continued*)

Declines					
Larkum and West (1990)	Botany Bay, NSW, Australia	Colour and B/W aerial photographs	2,500 ha	Presence/absence of seagrass mapped manually.	Historical aerial photographs from 1930–1985. 1942–1984: a steady decline and loss of 58% (257 ha) of *Posidonia australis* Causes were poor catchment management, dredging, and uncontrolled effluent disposal.
Ferguson and Wood (1993)	Core Sound, North Carolina, USA	Colour aerial photographs	20,000 ha	Minimum detection was 1 m diameter. Minimum mapping unit was 0.03 ha. Discontinuous seagrass was mapped if total area exceeded 0.03 ha; local texture indicated continuity or smooth gradients; and intervening unvegetated bottom were not large relative to the minimum mapping unit.	Between 1985 and 1988 seagrass loss of 6%.
Hastings et al. (1995)	Rottnest Island, Western Australia	Colour and B/W aerial photographs unrectified	Approximately 81 ha	Because of the small area of bays 1–2 aerial photographs were used in each bay. Seagrass was manually drawn onto mylar sheets which were scanned and polygon cover determined in ARC-INFO.	50 years of aerial photography was used Rocky Bay loss of seagrasses total 31% from mooring damage 18% 1941–1981 13% 1981–1992 Thomson Bay 1941–1992 <5% Fragmentation occurring.
Short and Burdick (1996)	Waquoit Bay, New Hampshire, USA	Colour aerial photographs	Approximately 300 ha	Mapping protocol was the same as Dobson et al. (1995).	40 ha (50%) loss of eel grass between 1987–1992 Loss associated with runoff of nutrients from housing estates.
Seddon et al. (2000)	Spencer Gulf, South Australia	Colour aerial photographs	70–80 km of coastline	Eight habitat categories including density of shoots and level of dieback Estimate of spatial area was 31 ± 30 ha.	Historical dieback between 1987 and 1994 in the intertidal and shallow subtidal Over 8,269 ha showed dieback attributed to climate change associated with El Niño.
Kendrick et al. (2002)	Cockburn Sound, Western Australia	Colour and B/W aerial photographs rectified and mosaiced	3,667 ha	As for Kendrick et al. (2000).	Historical decline in seagrass area by 77% since 1967. 1967–1972: 1,587 ha lost. 1972:1981: 602 ha lost. 1981–1999: 79 ha lost. Species of seagrass lost were predominantly *Posidonia sinuosa* and *P. angustifolia.*

sand blowouts was size specific with patches $<25\ m^2$ being colonised over a 50 year period, but larger patches remained the same size. The scaling of mapping studies of these slower growing species needs to capture these very slow expansion rates. Missing from landscape scale mapping studies are the appropriate temporal and spatial scales for observing recovery in seagrass meadows from known recruitment and growth rates of the specific seagrass species being studied.

There is a paucity of good rhizome growth data for many seagrass species. Rhizome production is difficult to study directly, and reconstruction methods have limitations. We have found that rhizome extension rates, branching rates, and mortality rates are not readily available for many seagrass species. Yet these growth measurements are important for interpreting expansion observed in mapping exercises and managing for recovery of seagrass meadows.

In summary, these mapping exercises have shown large-scale (up to 58%) losses due to environmental perturbations, but there have been gains of up to 21% shown in areas where recruitment has occurred or following removal of perturbation. We conclude that human impacts will tend to remove seagrass faster than it can recover, but recovery can and does occur.

IV. Case Study 1: Why did We Lose Seagrasses in Cockburn Sound Whereas Seagrass Area has Expanded on Neighbouring Parmelia and Success Banks?

A. Geographical and Historical Setting

Cockburn Sound and Success and Parmelia Banks are relatively protected marine waters to the south of Fremantle, Western Australia (Fig. 1). The sediment is unconsolidated carbonate sand and has formed largely from the onshore transport of sands over the past 7,500 years. Cockburn Sound is a sheltered marine embayment located to the south of Parmelia Bank. It is 16 km long by 9 km wide, and consists of a deep central basin (17–22 m deep) surrounded by shallow sandy platforms ranging in width from 50 m to 3 km, that support seagrasses (Fig. 1). Parmelia Bank is the northern boundary of Cockburn Sound and is approximately 4 km south of Success Bank. Success Bank extends in an east-west direction offshore just south of the port of Fremantle. Water depths where seagrasses are found are generally <10 m.

Prior to 1954, Cockburn Sound was used mainly for recreational purposes and commercial fishing, but its relatively protected deep waters also constituted an excellent anchorage, hence its choice as an outer harbour for the Perth-Fremantle area. Industrial development commenced with the establishment of an oil refinery in 1955, and the next 25 years saw the addition of iron, steel, alumina, and nickel refining or processing plants, chemical and fertiliser production plants, and a bulk grain terminal. With the development of the industrial complex, wharves and groynes were built and channels dredged for shipping access. A wastewater treatment plant was commissioned in 1966, which discharged south west of Woodman Point at the northern end of the Sound, while at the southern end of the Sound a rock fill causeway was built in 1971–1973 connecting Garden Island with the mainland. Industrial expansion resulted in deterioration of the Cockburn Sound environment, leading to extensive loss of seagrass. The Fremantle Port Authority (FPA) channel that enables shipping access into Cockburn Sound bisects Success and Parmelia Banks. This channel was originally dredged prior to the 1950s and maintenance dredging has been conducted occasionally since then. Shell sand dredging also occurs on Parmelia and Success Banks, and is a major threat to seagrass meadows in the region.

B. Seagrass Species

In 1999 in Cockburn Sound, seagrass beds were continuous over hectares and predominantly *Posidonia sinuosa* (and *Posidonia angustifolia*) with small areas of *Posidonia australis.* On Success and Parmelia Banks seagrass coverage was generally more spatially patchy and consisted of more equally represented assemblages than in Cockburn Sound. The seagrass species *Posidonia sinuosa*, *Posidonia australis*, *Posidonia coriacea*, *Amphibolis griffithii,* and *Amphibolis antarctica* occur as single- and mixed-species assemblages.

C. Loss and Recovery of Seagrasses

The decline in area of seagrass cover on shallow shelves that border Cockburn Sound was dramatic and the largest loss was concentrated over a 5 year

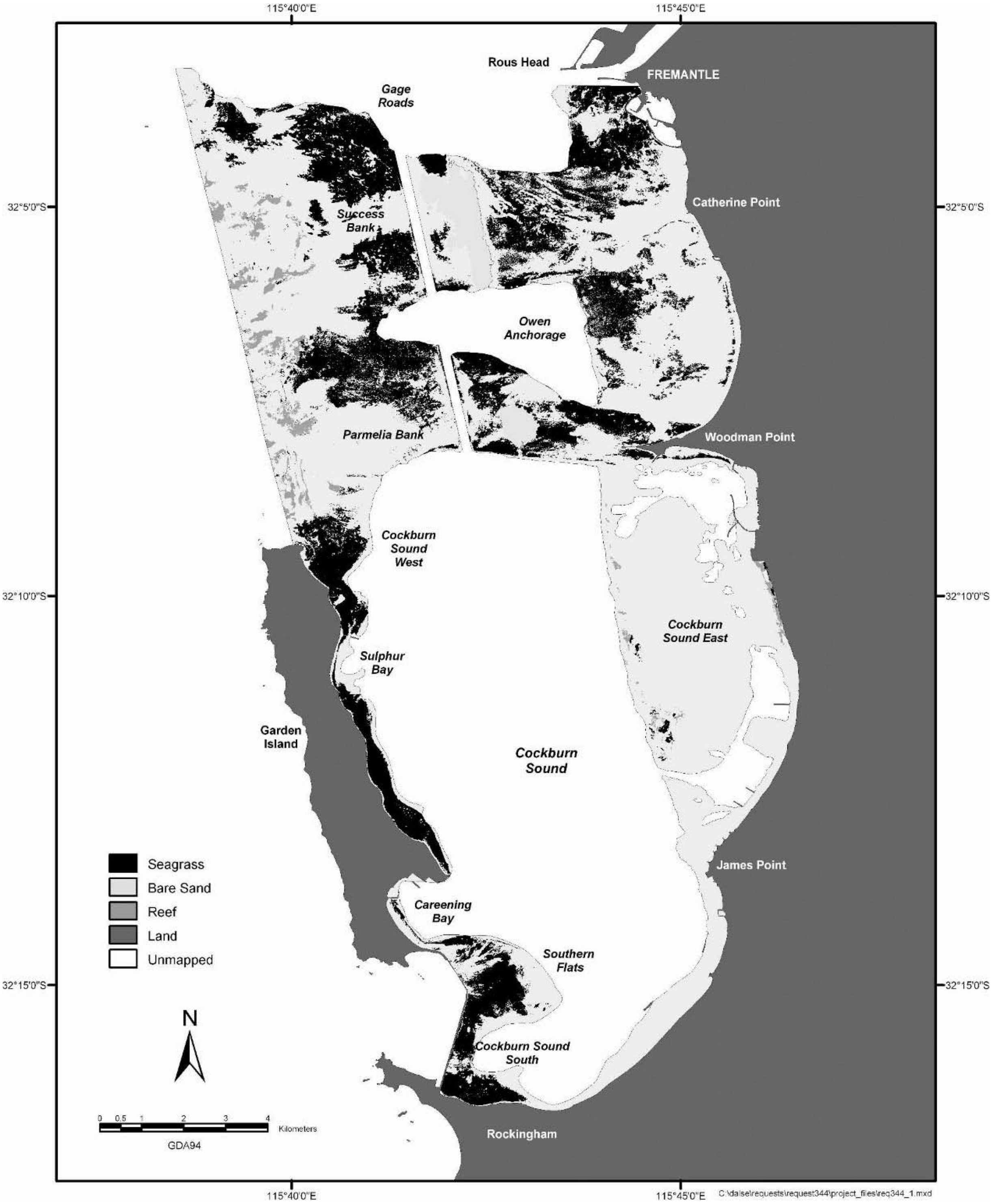

Fig. 1. Map showing the locations of Success Bank, Parmelia Bank, and Cockburn Sound, the extent of seagrass mapping bounded by the coastline and the 20 m isobath, locations mentioned in the text, and the 1999 mapped distribution of seagrasses and reef.

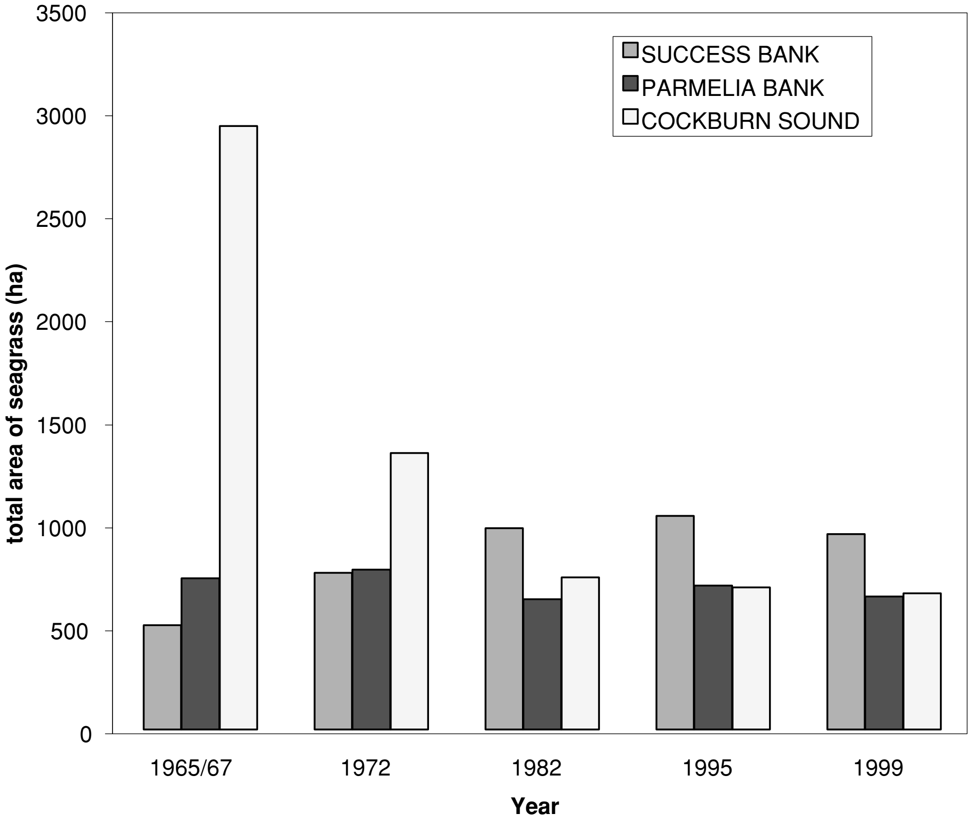

Fig. 2. Change in total seagrass coverage of waters <10 m deep for Success Bank, Parmelia Bank, and Cockburn Sound for 1965/1967, 1972, 1982, 1995, and 1999.

period between 1967 and 1972 (Cambridge et al., 1986; Kendrick et al., 2000) (Fig. 2). This 5-year time interval was effectively instantaneous for long-lived and slow growing species like *Posidonia sinuosa* and *P. australis*. The quantity of dead seagrass leaf and rhizome material that entered detrital pathways over the 5 year interval, over extensive areas of the eastern and southern fringing shelves, was immense, and probably fuelled the conversion of the inshore ecosystem from net autotrophic to net heterotrophic. Large losses of seagrasses continued into the 1980s and early 1990s. Since 1994 it appears that the total seagrass area in Cockburn Sound has remained relatively stable. In contrast, total seagrass area has remained relatively constant on Parmelia Bank, despite shell sand mining and pollution related losses of meadows bordering Cockburn Sound, and has doubled in area on Success Bank during the same time period (Kendrick et al., 2000) (Fig. 2). What broad scale mechanisms of seagrass expansion differ between these locations?

D. Mechanisms of Loss and Recovery

In Cockburn Sound, the seagrass species *Posidonia sinuosa*, *P. angustifolia*, and *P. australis* once formed an almost continuous bed between 1–6 m depth, which fringed the eastern, southern, and western flanks. By 1972 seagrasses had been lost or fragmented along the eastern and southeastern shores of the Sound. The construction of the Garden Island causeway, between 1971 and 1973, reduced the wave energy experienced on the Southern Flats and appears to have exacerbated the losses of seagrasses in this area. The losses of seagrasses in the deeper waters on the eastern edge of Cockburn Sound between 1972 and 1999 have been associated with the initial decline in water quality and the change from predominantly a system driven by benthic primary producers, to dominance of pelagic primary producers. Port developments by the Australian Navy in Careening (1972–1974) and Sulphur (1976–1978) Bays resulted in additional seagrass loss in the Cockburn Sound West region (Cambridge and McComb, 1984). Seagrass losses in this region have also occurred along the deeper waters which is most likely related to reduction of light associated with the decline in water quality in the Sound (Cambridge et al., 1986). On the shallow *Posidonia sinuosa* meadows north of Sulphur Bay a 3 ha rectangular area of seagrasses was lost between 1981 and 1994 to grazing sea urchins *Heliocidaris erythrogramma* and *Temnopleuris michaelsenii* and again in 1991 (Bancroft, personal communication). Loss of seagrass meadows due to invasions by *Temnopleuris michaelsenii* were previously reported near Rockingham in 1972, Careening Bay in 1973, Woodman Point in 1976 and Warnbro Sound in 1978 (Cambridge et al., 1986). There have also been some increases in seagrass cover in Cockburn Sound: Cambridge (1975) reported crescentic sand blowouts on Southern Flats, which are now continuous meadows of *P. sinuosa*.

In contrast to the main basin of Cockburn Sound, seagrass meadows on Success and Parmelia Banks show both measurable gains and losses in coverage. The gain in coverage between 1965 and 1999 is significant, and demonstrates that colonisation by slow-growing seagrass species is measurable at a map scale of 1:10,000 over the mapping period (35 years). The seagrass assemblages that account for most of the gains in coverage were *Amphibolis griffithii* and *Posidonia coriacea*. The gains have predominantly been associated with increases in the size of existing patches at the limit of the mapping resolution (30 m^2) and in infilling, and coalescence of seagrass patches into larger continuous meadows. Some increases in coverage of *Posidonia sinuosa* and *Posidonia australis* on Parmelia Bank were associated with regrowth of shoots from pre-existing rhizome matte. In several areas, the gains and losses of seagrass coverage were associated with the spatial displacement of sand blowouts through beds. The mechanism behind loss and recovery over much of Success and Parmelia Bank appears to be that the gains and losses in seagrass coverage are in dynamic equilibrium, and largely responding to sediment movements. Sediment movement through seagrass beds, in the form of subaqueous bed forms (sand bars), influences the survival and growth of seagrasses as they are sensitive to both burial (Marbà et al., 1994; Marbà and Duarte, 1995) and erosion (Patriquin, 1975; Clarke, 1987). As a result, landscape-scale displacement of seagrasses in the direction of the prevailing currents is occurring over decades in the Success Bank East and West and Parmelia Bank West regions. A similar process was observed in Holdfast Bay, South Australia, where it was estimated that a full turnover of habitat would occur between sand blowouts and beds of *Posidonia* spp. in 140 years (Clarke, 1987; Clarke and Kirkman, 1989). Clarke (1987) also estimated maximum movements of blowouts in Holdfast Bay of 1 m year^{-1} during a 32-year period. This rate of movement is similar to the erosion rates of 1.2 to 1.5 m year^{-1} measured from sand blowouts in *Thalassia testudinum* beds in the West Indies (Patriquin, 1975). Yet it is 10 times less than that recorded for sand bar movements through beds of *Cymodocea nodosa* (13.0 ± 0.6 m year^{-1}) in the Mediterranean (Marbà et al., 1994; Marbà and Duarte, 1995).

The sand bar migrations ensure that seagrass species are in a continuous state of colonisation, and may account for the dominance of *Amphibolis griffithii* and *Posidonia coriacea* assemblages on Success Bank. The greatest increases in seagrass coverage in the Success and Parmelia Bank region were predominantly from the *Amphibolis griffithii* and *Posidonia coriacea* assemblages (Kendrick et al., 2000), although the published rhizome extension rates for these species (Clarke and Kirkman, 1989) cannot fully account for these increases (Kendrick et al., 1999).

When introducing the case study, we raised the question of why we lost seagrasses in Cockburn Sound whereas seagrass area has expanded on neighbouring Parmelia and Success banks. The reason for loss in the Sound clearly lies in eutrophication (Silberstein et al., 1986), which accompanied industrial development, possibly exacerbated by a minor reduction in the already limited exchange between basin and ocean through causeway construction. Eutrophication combined with the dominance of *P. sinuosa*, a slow growing meadow forming seagrass, resulted in extensive loss and little recovery over 30 years. In contrast, although eutrophication occurred on Parmelia Bank (Silberstein et al., 1996) and to a lesser degree Success Bank, the mixture of faster growing colonising species combined with slower growing, monospecific meadow-forming species, greater hydrodynamic forcing and therefore higher flushing rates and large scale sand movement, all suggest the seagrasses on Parmelia and Success Banks are in dynamic equilibrium with their environment. This has resulted in greater resilience to large spatial-scale losses in the seagrass assemblages over the same 30-year period.

Patch dynamics studies of temperate Australian seagrasses have been limited (Clarke, 1987; Kendrick et al., 1999). Elsewhere in the world, patch dynamics studies have predominantly focussed on fast growing seagrass species like *Zostera*, *Cymodocea*, *Thalassia*, and *Halodule* (Vidondo et al., 1997; Ramage and Schiel, 1999; Turner et al., 1999; Robbins and Bell, 2000). These studies have all demonstrated that seagrass patches may move several meters within a year and at rates faster than that recorded for the growth of individual rhizomes. Large-scale seagrass losses continue to occur as a result of natural processes (such as sand inundation) and human activities (presently mainly associated with eutrophication and, on Success Bank, shell-sand dredging).

V. Case Study 2: Florida Bay

Changes, both declines and recoveries, are also apparent in Florida Bay. Florida Bay is a large (19,000 km^2), shallow (<2 m depth), carbonate system dominated by *Thalassia testudinum*, growing over 90% of subtidal mud banks and basins (Zieman et al., 1989). Seagrasses in Florida Bay have been the subject of intensive and consistent studies over the last 15–20 years (Zieman et al. 1989; Fourqurean et al., 1992a,b, 1995; Hall et al., 1999; Durako et al., 2002). A mass mortality (die-off) event in 1987, when 4,000 ha of *Thalassia* died and 24,000 ha were affected, was attributed to the combination of a protistan pathogen, *Labyrinthula* (Durako and Kuss, 1994), sulphide toxicity (Carlson et al., 1994), elevated water temperatures (Hall et al., 1999) and salinity increases (to 50 psu) (Zieman et al., 1999). The salinity increase, following alterations to the hydrology (canal dredging, dike building in the Everglades) and several years of drought in southern Florida, appeared to be the major environmental contributor to the die-off of *Thalassia* (Fourqurean et al., 1995). *Thalassia*-dominated subtidal areas were initially replaced by *Halodule wrightii* (Fourqurean and Robblee, 1999). Following the return to more normal rainfall conditions in the early 1990s, all seagrasses were then affected by phytoplankton and algal blooms that reduced light climate available for seagrass growth and lead to losses of not just *Thalassia* and *Halodule,* but also of *Syringodium filiforme* (Hall et al., 1999).

Subsequent monitoring has demonstrated extensive changes in seagrass populations across Florida Bay (Durako et al., 2002). For example, chronic turbidity in western Florida Bay leads to an increase in distribution and abundance of low-light adapted species such as *Halodule wrightii* and *Halophila engelmanii* (Durako et al., 2002).

These changes have been documented by extensive systematic random sampling using the Braun-Blanquet frequency/abundance technique (Mueller-Dombois and Ellenberg, 1974), a rapid semi-quantitative visual assessment, at over 300 sites in Florida Bay, over a 10-year period (1995–2004). Spatial trends in the Braun-Blanquet data have been mapped using a Krigging algorithm (Durako et al., 2002), and total basin-level species abundances have been calculated from the krigged grid data (Table 3). These abundance maps reveal that although *Thalassia* is still the dominant genus in Florida Bay, it has not recovered its pre-decline distribution; *Halodule* abundance has dramatically increased, so that the previous five fold abundance of *Thalassia* over *Halodule* is now only three fold (Durako et al., 2002). Zieman (1982) suggested that, historically, *Halodule* was more abundant and that *Thalassia* increases in Northeast Florida Bay, prior to the die-off, resulted from the alterations to the hydrology increasing salinities in Florida Bay (“lagoonization”).

Many studies on the possible mechanisms of seagrass loss, as well as continued monitoring of seagrass and macro-algal distributions in Florida Bay have been conducted. There is currently an attempt to manage the hydrology of Florida Bay to minimize the occurrence of hypersaline conditions, as part of the Comprehensive Everglades Restoration Program (CERP), a 10-year $8 billion ecosystem restoration program. One of the goals of CERP is to sustainably maintain the seagrasses in Florida Bay, especially *Thalassia,* via engineering solutions to manage drainage. Restoration efforts in this changing system will be challenged by the effects of increasing population pressures on Florida Bay, especially in terms of increasing water demands.

VI. Species-Specific Recruitment and Growth Characteristics

Clearly, species-specific traits in clonal growth and seedling recruitment play a large role in the timing

Table 3. Relative abundances of *Thalassia testudinum* and *Halodule wrightii* in 10 Florida Bay Basins from spring 1995 to spring 2003 as determined by Braun-Blanquet sampling and summation of krigged data (see Durako et al., 2002; most recent data Durako, personal communication 6/04).

	1995		1996		1997		1998		1999		2000		2001		2002		2003	
Basin	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw	Tt	Hw
Blackwater Sound	30.0	11.8	35.5	9.2	52.1	18.8	44.3	28.6	58.5	18.6	58.9	18.2	40.4	12.2	41.4	17.1	38.2	14.4
Calusa Key	38.7	0.0	44.7	5.1	28.5	4.5	38.5	6.3	43.7	7.1	36.3	10.7	28.2	7.7	41.3	10.0	39.8	9.2
Crane Key	26.0	2.9	27.3	2.4	32.9	4.3	26.8	5.6	33.7	4.3	38.8	5.1	16.7	2.2	26.1	4.9	23.4	3.1
Eagle Key	57.3	28.2	72.9	26.2	50.0	21.7	85.8	29.6	75.1	23.1	16.1	29.2	39.3	25.8	62.2	26.9	81.7	24.7
Johnson Key	12.8	6.1	23.5	13.1	17.2	20.5	10.1	25.0	12.6	27.7	28.2	41.0	28.3	20.8	31.5	24.2	36.4	21.1
Madiera Key	16.1	6.3	22.4	4.1	23.0	6.0	27.2	4.2	35.3	4.7	35.7	6.1	17.3	2.3	29.6	4.5	18.0	2.0
Rabbit Key	128.9	10.0	125.0	10.7	105.3	11.8	94.4	24.7	109.5	48.4	94.2	32.8	86.6	29.0	111.3	31.6	108.8	21.1
Rankin Lake	3.9	3.9	3.8	3.6	3.6	8.7	20.7	7.5	4.8	7.7	5.9	6.6	5.9	9.1	5.4	3.2	11.6	3.5
Twin Key	159.8	11.3	122.7	17.7	105.8	25.3	142.7	20.7	137.5	21.2	126.4	18.3	111.9	16.2	104.8	19.0	124.5	15.8
Whipray Bay	16.8	6.2	29.0	6.6	31.5	8.0	30.6	12.6	47.3	28.7	45.1	15.8	29.0	10.8	38.0	14.0	31.4	9.4
Total	490.3	86.8	506.8	98.8	449.8	129.6	521.2	164.9	558.0	191.5	545.7	183.8	403.7	136.1	460.7	155.5	513.8	124.5

and extent of seagrass recovery. The following section summarizes our present knowledge on seedling recruitment and clonal growth for a selection of seagrass species and complements the more detailed presentation in Chapters 5 and 11.

Rates of loss/recovery are strongly linked to lifespan, clonal growth, and seedling recruitment of specific species of seagrasses. The temporal and spatial scales of rates of plant growth determine human perceptions of observed patterns of changes in seagrass landscapes. For example, *Zostera* regrowth is often rapid, in months to years (Baldwin and Lovvorn, 1994), as is *Halodule* (Williams, 1988; Robbins and Bell, 2000) whereas *Posidonia* species only regrow at the scale of decades (Shepherd et al., 1989; Kirkman and Kuo, 1996; Meehan and West, 2000). Long-lived meadow forming genera such as *Posidonia* and *Thalassia* are recorded as not returning from disturbance. Recovery is often a process that takes decades (Duarte, 1995), but the loss process is perceived as being more rapid, given our often poor ability to detect initial declines in seagrasses. Despite human perceptions, scales of decline for seagrasses are comparable with scales of their recovery if the original cause of loss is removed. Unfortunately, for *Posidonia* species this would require that perturbations occurred less than once a century (Duarte 1995), which does not correspond with the observed rates of loss (see Cambridge and McComb, 1994; Silberstein et al., 1996; (Western Australia) Pergent and Pergent-Martini, 1991; Marba and Duarte, 1997 (Mediterranean)).

VII. Can Seagrass Management be Proactive?

Effective management of seagrasses requires detailed understanding of their distributions, growth rates, and rates of change under natural conditions, integrating information on rates of seedling recruitment, clonal expansion, and recovery of habitat conditions, and consideration of the changes of these rates during recovery. In addition, knowledge of threshold values of decline drivers is essential to define effective management polices to prevent irreversible, at least at human timescale, seagrass losses. Few areas of the world have this detailed knowledge. Seagrass protection requires at least prevention of their destruction by coastal engineering works or other physical impacts (see Duarte et al., 2003 for a review), and, more importantly, reduction of organic and nutrient inputs as well as maintenance of light (at 20% of surface irradiance, Dennison et al., 1993) to ensure an adequate light climate.

Seagrass management is inadequate on a global scale. Over the last two decades, the loss of seagrass from direct and indirect human impacts amounts to 18% of the documented seagrass area (Green and Short, 2003). Seagrass losses occur as development pressure on coastlines increases. As well as direct impacts, use and development of catchments creates indirect impacts on otherwise highly regulated seagrass areas. Effectiveness of protection of seagrass in marine protected areas is still unclear. Assessments of recovery of *Posidonia oceanica* beds in Cabrera Archipelago National Park (Spain) concluded that while regulation has improved the status of seagrasses in the park, recovery is a very slow process requiring centuries to be completed, and will be threatened by organic inputs from visitors to the park (Marbà et al., 2002). Documenting such responses requires effective monitoring programs.

Landscape scale mapping studies (see also Bell et al., Chapter 26) require the setting of appropriate time and space scales for observing recovery in seagrass meadows from known recruitment and growth rates of the specific seagrass species being studied. Unfortunately, many managers of coastal environments regard seagrass distributions as being fixed and static over a human lifespan whereas the evidence suggests they are not (see Chapters 24, 25, and 26).

Seagrass can be viewed as migrating through shallow subtidal or intertidal habitat (see Chapters 5, 11, and 26), and as the boundaries of seagrass meadows and patches are not static, coastal habitat may be regarded as potential seagrass even when there is no seagrass present (see Chapters 25, 26). Human impacts, particularly resulting in eutrophication and increased sedimentation, will increase seagrass losses worldwide (Duarte et al., 2003). Potential seagrass habitat is now being recognised by legislation in some countries, and if management is effective, the rates of seagrass recolonisation, as documented in this chapter, can proceed. The balance, however, is still toward seagrass decline.

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Chapter 24

Human Impacts on Seagrasses: Eutrophication, Sedimentation, and Contamination

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I. Introduction

Growth of human populations along coastal environments, as well as poor water management practices have resulted in the complete loss of seagrass meadows (Kemp et al., 1983; Larkum and West, 1990; Short and Wyllie-Echeverria, 1996; Peters et al., 1997). For example, the catastrophic loss of seagrasses clearly illustrated in Fig. 1 is linked to coastal development and associated reduction in water quality. However, it is now being recognized that seagrasses can be moderately tolerant of anthropogenic contamination and recovery of meadows is being documented (e.g. Bricker et al., 1999; Kurz et al., 1999; Tomasko, 2002; Walker et al., Chapter 23). Seagrasses growing in estuaries are particularly vulnerable to contamination from anthropogenic sources, more so than coastal seagrasses.

Contamination in the estuary can arise from discrete point sources (e.g. industrial waste) or diffuse non-point contamination (e.g. catchment runoff); whereas, seagrasses growing in shallow coastal habitats can be damaged by shipping traffic, contaminated bilge water, accidental spills, and contaminated by antifouling compounds. Generally, seagrass loss is well documented; however, little is known

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Fig. 1. Aerial photographs from Old Tampa Bay, Florida USA. The 1948 image (LHS) shows extensive seagrass meadows in the shallow waters bisected by three small creeks. The image of the same region in 1999 (RHS) shows almost no seagrass remaining in previously colonized areas.

about how seagrasses respond to, tolerate and recover from anthropogenic contamination. Causality is rarely established for the loss of a particular meadow and factors contributing to a decline are more often established through correlation and corroborating results from experimental studies. This was highlighted when Short and Wyllie-Echeverria (1996) reviewed global impacts on seagrasses, and recognized that little is known about toxic impacts on seagrasses leading to a poor understanding of tolerance/resistance mechanisms. This chapter will provide an overview of the current understanding of how anthropogenic contaminants impact seagrasses, the ecophysiological responses of seagrasses (Table 1) and finally describe how modeling can be used to manage contaminant loads (specifically nutrients) in the process of seagrass recovery.

II. Anthropogenic Stressors

Anthropogenic stress can be linked to any number of processes associated with human activity, from water diversion changing salinity gradients in estuaries to the most recent herbicide, designed to knock out the photosynthesis of terrestrial weeds whilst having a limited impact on non-target aquatic species. Of all human impacts, eutrophication has possibly the most widespread impact on seagrasses. Nutrients have also been shown to have a toxic effect (Burkholder et al., 1992; van Katwijk et al., 1997), in addition to promoting the growth of phytoplankton and epiphytic macroalgae, which ultimately block light penetration to the seagrass (Neverauskas, 1988; Shepherd et al., 1989; Dennison et al., 1993; Short et al., 1995; McGlathery, 2001). Runoff is usually linked with increased nutrient loads within the catchment; however, sedimentation can have an equally damaging impact on seagrasses. Urban development brings a cacophony of anthropogenic contaminants; these can be broadly grouped as heavy metals, herbicides and pesticides, and petrochemicals. In addition to these, the sudden extreme reductions in salinity, associated with freshwater runoff, may also act as a co-stressor along with the effects of nutrients, sediments and other contaminants discharged into the marine coastal environment. Yet, little is known about the interactive effects of various anthropogenic stressors and whether natural factors, such as temperature and salinity, act synergistically with these anthropogenic stressors causing enhanced seagrass mortality.

A. Nutrients

While a number of studies have shown a positive correlation between nutrient availability and seagrass biomass and/or productivity (e.g. Short et al., 1985,

Table 1. Recent experimental studies investigating the contribution of eutrophication, sedimentation and contamination toward the decline of seagrass condition and survival.

Impact type	Species	Location	Endpoint	Reference
Nutrients				
Water column nutrients	*Z. marina, Halodule wrightii, R. maritima*	SE (North Carolina) USA	Survival, growth, shoot density	Burkholder et al. (1992, 1994)
	Zostera marina	NE (New Hampshire) USA	Growth, morphology	Short et al. (1995)
	Z. marina	SW Netherlands	Survival, morph, phenolics	van Katwijk et al. (1997)
	Z. marina	E (Chesapeake Bay) USA	Growth	Moore and Wetzel (2000)
	Z. noltii	Cádiz Bay, Spain	Growth, production	Brun et al. (2002)
Sediment nutrients	*Cymodocea serrulata, H. uninervis, Z. capricorni*	E (Moreton Bay) Australia	Growth, morphology, physiology,	Udy and Dennison (1997b)
	Halodule uninervis	NE (Green Island) Australia	Growth, morph, physiology	Udy et al. (1999)
Sediments				
Turbidity	*Halophila ovalis, H. pinifolia*	Gulf of Carpenteria, Australia	Survival, morphology, physiology	Longstaff and Dennison (1999)
	Z. marina	NE (Chesapeake Bay) USA	Growth	Moore and Wetzel (2000)
Sedimentation	*C. rotundata, C. serrulata, E. acoroides, Halodule uninervis, S. isoetifolium, T. hemprichii*	Philippines	Survival, morphology	Duarte et al. (1997)
Herbicides				
Atrazine	*Z. marina*	NE (Chesapeake Bay), USA	Photosynthesis	Correll and Wu (1982)
	Z. marina	NE (Chesapeake Bay), USA	Growth, mortality	Delistraty and Hershner (1984)
	H. ovalis	E Australia	Fluorescence	Ralph (2000)
	Z. marina	NE (Chesapeake Bay), USA	Growth	Schwarzschild et al. (1994)
	Z. capricorni	E Australia	Fluorescence	Macinnis and Ralph (2003a)
DCMU (Diuron)	*H. ovalis*	E. Australia	Fluorescence	Ralph (2000)
	H. ovalis, Z. capricorni, C. serrulata	E. Australia	Fluorescence	Haynes et al. (2000b)
	Z. capricorni	E. Australia	Fluorescence	Macinnis and Ralph (2003a)
Irgarol	*Z. marina*	UK	Fluorescence	Scarlett et al. (1999)
	Z. capricorni	E. Australia	Fluorescence	Macinnis and Ralph (2003a, 2004)
Glyphosate	*H. ovalis*	E. Australia	Fluorescence	Ralph (2000)
Simazine	*H. ovalis*	E. Australia	Fluorescence	Ralph (2000)
Heavy metals				
Copper	*H. ovalis*	E. Australia	Fluorescence	Ralph and Burchett (1998)
	H. ovalis, H. spinulosa, Halodule univervis, Z. capricorni, C. serrulata	E. Australia	Fluorescence	Prange and Dennison (2000)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2002, 2004)
	Z. capricorni	E. Australia	Photosynthesis	Conroy et al. (1991)

(*continued*)

Table 2. (cont.)

Impact type	Species	Location	Endpoint	Reference
Zinc	*Z. capricorni*	E. Australia	Photosynthesis	Conroy et al. (1991)
	H. ovalis	E. Australia	Fluorescence	Ralph and Burchett (1998)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2002, 2004)
	H. ovalis, H. spinulosa, H. univervis, Z. capricorni, C. serrulata	E. Australia	Fluorescence	Prange and Dennison (2000)
Lead	*Z. capricorni*	E. Australia	Photosynthesis	Conroy et al. (1991)
	H. ovalis	E. Australia	Fluorescence	Ralph and Burchett (1998)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2002)
Cadmium	*H. ovalis*	E. Australia	Fluorescence	Ralph and Burchett (1998)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2002)
Petrochemicals				
Crude oil	*P. australis*	E. Australia	Morphology, photosynth	Hatcher and Larkum (1982)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2003b)
	H. ovalis	E. Australia	Fluorescence	Ralph and Burchett (1998)
	Halodule wrightii, S. filiforme, T. testudinum	Florida, USA	Growth	Thorhaug et al. (1986)
	Halodule uninervis, H. ovalis, H. stipulacea	Middle East	photosynth, respiration	Durako et al. (1993)
	Thalassia, Halodule, Syringidium	Caribbean	Growth	Thorhaug (1988)
	Z. noltii/augustifolia	Milford Haven, UK	Percent cover	Howard et al. (1989)
Dispersant	*Posidonia australis*	E. Australia	Morphology, photosynth	Hatcher and Larkum (1982)
	H. ovalis	E. Australia	Fluorescence	Ralph and Burchett (1998)
	Z. capricorni	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2003b)
	Z. noltii/augustifolia	Milford Haven, UK	Percent cover	Howard et al. (1989)
	Thalassia, Halodule, Syringidium	Caribbean	Growth	Thorhaug (1988)
Oil + dispersant	*Z. capricorni*	E. Australia	Fluorescence	Macinnis-Ng and Ralph (2003b)
	Z. noltii/augustifolia	Milford Haven UK	Percent cover	Howard et al. (1989)
	Halodule wrightii, S. filiforme, T. testudinum	Caribbean	Growth	Thorhaug et al. (1986)
	H. ovalis	E. Australia	Fluorescence	Ralph and Burchett (1998)

1990; Powell et al., 1989, 1991), most assessments have concluded that increased nutrient loading of estuarine and nearshore marine waters is more of a detriment than a benefit to seagrass ecosystems and the fisheries they support. Studies in Denmark (Borum, 1985), France (Bourcier, 1986), Australia (Larkum, 1976; Cambridge et al., 1986; Silberstein et al., 1986), Mexico (Flores-Verdugo et al., 1988; Reyes and Merino, 1991), and the USA (Kemp et al., 1983; Orth and Moore, 1984; Lapointe et al., 1994; Short and Burdick, 1996; Tomasko et al., 1996; Valiela et al., 1997; Tomasko et al., 2001) are but a few of the many assessments that have concluded that anthropogenic increases in nutrient loading of the water column are inversely related to various indices of seagrass health.

1. Sources of Nutrients

Eutrophication is one of the most widely reported causes of anthropogenic seagrass decline and continues to pose the greatest threat to seagrass populations (Short and Wyllie-Echeverria, 1996). Increased urbanization worldwide had led to greater discharges of domestic and industrial waste into rivers, estuaries and coastal waters. Nitrogen and phosphorus are the primary nutrients causing eutrophication, which in seawater, most commonly occurs in the form of excess nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}). Major anthropogenic sources of these nutrients include sewage effluent, septic system seepage, stormwater outfalls, industry (abattoirs, steel works, fertilizer processing plants), aquaculture (particularly sea cage-culture and prawn farms), and agricultural runoff. For example, point sources (both wastewater treatment plants and industry) account for approx. 10 and 13% of the present day nitrogen load into Sarasota and Tampa Bays, with stormwater runoff accounting for 56 and 45% of the load, respectively (Heyl, 1992; Zarbock et al., 1996). In contrast, point sources were not a significant source of nitrogen loads into Lemon Bay (Florida), where stormwater runoff is thought to account for ~76% of the annual N load, followed by septic tank systems (14%) (Tomasko et al., 2001).

Strong causal links have been established between seagrass loss and eutrophication. For example, between 1938 and 1976, nitrogen loads into Tampa Bay increased from 1,737 kg Total Nitrogen (TN) year^{-1} to 8,985 kg TN year^{-1}, a more than five-fold increase (Tampa Bay National Estuary Program [TBNEP], 1996). In adjacent Sarasota Bay, nitrogen loads in 1988 were estimated to be 905 kg TN year^{-1}, a value nearly five-times higher than estimated loads prior to development of the watershed (Sarasota Bay National Estuary Program [SBNEP] 2000). In response to both the direct impact from dredging activities, as well as reduced water clarity due to nutrient-induced increases in phytoplankton abundance, seagrass coverage in both Tampa Bay and Sarasota Bay decreased precipitously from early estimates (Tomasko et al., 1996; Johansson and Greening, 1999, respectively).

2. Process of Nutrient Contamination and Eutrophication

Seagrass beds exposed to eutrophication have been reported to exhibit symptoms such as high epiphytic loading, low shoot densities, low leaf area indices, and low biomass (Tomasko and Lapointe, 1991; Delgado et al., 1999; Walker et al., Chapter 23), although the mechanisms of decline can vary both spatially and temporally. The cause/effect relationships between nutrient enrichment and seagrass response are complex and are likely related to both the rate at which nutrients are made available to seagrass beds, as well as the absolute concentrations. Factors such as the flushing rate of receiving waters have a significant role in determining the persistence of nutrients within a system. Estimates of residence time are considered a major factor for determining the susceptibility of an estuary to nutrient enrichment (Bricker et al., 1999). In an hypothetical example where water volumes and nutrient loads into an estuary would be similar, the degree of expression of eutrophic conditions would be less in the better-flushed estuary, and greater in the estuary with the longer residence time (Bricker et al., 1999). Moore and Wetzel (2000) have also suggested that in some situations, pulsed high levels of nitrogen into waters with limited turnover may have a greater impact than long-term moderate concentrations.

Two important processes have been linked to eutrophication-related decline in seagrasses; shading by phytoplankton and overgrowth by epiphytes, both result in a reduction in the light reaching the seagrass. The dominant impact of eutrophication is mostly due to phytoplankton-induced reductions in water clarity, which in some instances is further compounded by direct impacts such and dredge and fill activities (Lewis et al., 1991; Udy and Dennison, 1997a; Johansson and Greening, 2000). Although studies by Borum (1985), Silberstein et al. (1986), Neverauskas (1987) and Dixon (1999) demonstrate the important role played by epiphytic algae in reducing light penetration to the leaves of seagrasses in eutrophied waters, and overgrowth by macroalgae has also been implicated as a mechanism of nutrient-induced seagrass declines (Lapointe et al., 1994; Valiela et al., 1997; Hauxwell et al., 2001; Deegan et al., 2002). Regardless of the mechanism(s) of impact, nutrient enrichment of nearshore marine and estuarine waters is thought to be the major reason for seagrass loss worldwide (e.g. Larkum, 1976; Kemp et al., 1983; Cambridge and McComb, 1984; Orth and Moore, 1984; Bourcier, 1986; Silberstein et al., 1986; Kenworthy et al., Chapter 25).

3. Status of Eutrophication

During the 1960s to 1980s, there were a number of significant eutrophication related declines of sensitive species, including *Posidonia* spp. and *Amphibolis* spp. in Australia (Higginson, 1970; Cambridge and McComb, 1984; Bastyan, 1986; Shepherd et al., 1989; Larkum and West, 1990; Hillman et al., 1991) and *Posidonia oceanica* in Europe (Peres and Picard, 1975; Pergent-Martini and Pergent, 1996). This era represented a time where untreated sewage and industrial waste were discharged directly into coastal waters and estuaries without understanding of the detrimental nature of nutrients on seagrass meadows. In response to work investigating these declines, management of water resources and wastewater has greatly improved in some areas, although non-point source (i.e. stormwater runoff) pollution loads remain much more difficult to control than point sources (e.g. Heyl, 1992). We are now able to accurately predict that, for example, in Lemon Bay a 45% increase in N loading by 2010 is likely to increase both chlorophyll levels and light attenuation, resulting in an average reduction in the depth limit of light-limited meadows of *Thalassia testudinum* by approximately 24%, from 1.2 m (MTL) to 0.9 m (Tomasko et al., 2001). Unless future nutrient load reductions occur, seagrass meadows around the world are likely to experience nutrient-induced decreases in seagrass coverage (den Hartog and Polderman, 1975; Orth and Moore, 1983; Johansson and Greening, 1999; Tomasko et al., 1996).

4. Ecophysiology of Nutrient Effects on Seagrass

The detrimental effects of light attenuation on seagrass, whether due to direct shading from algal epiphytes and macroalgal smothering or indirect effects of phytoplankton, was suggested by Shepherd et al. (1989) as the key unifying hypothesis explaining the primary cause of seagrass declines worldwide. However, in the last decade the contribution of direct nitrogen toxicity and sediment anoxia (sediments contaminated with organic matter waste) as mechanisms of mortality have been receiving more attention. Research into nitrogen as a toxicant per se, has been a topic of inquiry since the study by Burkholder et al. (1992) pointed out the potential for a direct toxic effect of elevated levels of water column nitrate to seagrass meadows in nearshore waters of North Carolina (USA). While a small degree of nutrient enrichment can enhance seagrass growth, further enrichment may lead to a situation of nutrient saturation and even toxicity. Seagrasses exposed to nutrient saturation have been shown to exhibit high tissue nutrient content and amino acid concentrations (Udy and Dennison, 1997a) and such precursors can alert researchers and managers to the possibility of broad-scale decline.

The paradox is that nutrients are essential for seagrass photosynthesis and growth. In fact, it has been shown that seagrass meadows can be N, P, and/or Fe limited, possibly to the detriment of the bed (Dennison et al., 1987; Udy and Dennison, 1997a). For example, nitrogen limitation was a significant factor contributing to the sudden decline of *Zostera marina* in Grevelingen, The Netherlands (van Lent et al., 1995). Consequently, considerable effort has been directed toward the determination of N and P requirements and nutrient budgets in areas where nutrient levels are sub-optimal and positive physiological and ecological effects have been reported in response to nutrient enrichment experiments (e.g. Udy and Dennison, 1997a). Typically, seagrasses that are nutrient-limited, react positively to fertilization experiments showing responses including increased growth rates, enhanced photosynthetic performance, increased leaf length, higher shoot densities, and increased above ground biomass (e.g. Agawin et al., 1996; Udy and Dennison, 1997b). Agawin et al. (1996) pointed out a link between C incorporation and nutrient deficiency, proposing that since chlorophyll synthesis is dependent upon nutrient supply, therefore fertilizing N-limited seagrasses can lead to enhanced photosynthetic rates, lower respiration rates and increased photosynthetic efficiency.

The most common symptoms of eutrophication-related seagrass decline include high epiphytic loading (but see Mateo et al., Chapter 7, Borowitzka et al., Chapter 19 and Valentine and Duffy, Chapter 20 for the offsetting effects of grazing) slower growth rates, reduced biomass, and shoot thinning (Cambridge et al., 1986; Short et al., 1995); although some of these variables do not always respond consistently to elevated nutrients. For example, in a study of morphological and physiological characteristics of *Zostera capricorni* in Moreton Bay (Australia), there were no significant differences in leaf length, shoot density, biomass, and growth rates relating to increased nutrients, whereas leaf nutrient content and amino acid concentration increased with greater proximity to various nutrient sources, such as river runoff, local septic systems, sewage, and prawn farm effluent (Udy and Dennison, 1997a). Additionally, research indicates that not all species are similarly vulnerable to high levels of nutrients. Burkholder et al. (1994) suggested that some species have developed mechanisms to regulate the metabolism of nitrate. In this experiment, shoot production of *Halodule wrightii* and *Ruppia maritima* greatly increased in response to nitrate enrichment, while *Zostera marina* responded more typically with reduced shoot production, although at this stage the mechanisms to enable nitrate regulation are not clear.

Factors such as light availability, temperature, balance of C, N, P, and redox potential all affect the ability of seagrasses to deal with excessive nutrients. The impact of other factors such as reduced salinity combined with elevated nutrients is currently unknown. This is important because many sources of nutrients are delivered in freshwater (e.g. river runoff and sewage). While many species have proven to be fairly tolerant of a broad range of salinities, negative symptoms such as loss of biomass and lack of leaf production have occurred in salinities lower than 10 ppt (Hillman et al., 1995; Doering and Chamberlain, 1999) and it is not clear whether these effects would be exacerbated in conditions of elevated nutrients. Interactive effects are likely, as Tomasko and Hall (1999) found in a field study that *Thalassia testudinum* productivity was depressed at salinities less than 20 ppt; however, in this system, low salinity was associated with elevated dissolved organic matter, rather than suspended sediments.

5. Water Column Nutrients

In addition to the major effect of eutrophication induced light attenuation outlined earlier, a direct toxic effect of water-column nitrogen on the physiology of seagrasses was demonstrated by Burkholder et al. (1992). They found signs of 'crumbling' shoot meristems preceding whole plant mortality for *Zostera marina* in the medium and high enrichment treatments exposed to daily doses of the nitrate (7 and 35 μM N-NO_3^- respectively) over an 8 week period. Burkholder et al. (1994) hypothesized that the lack of an inhibition mechanism for nitrate uptake may eventually result in internal imbalances of other essential nutrients (e.g. C and P) and that this could be a result of the plants need to sequester carbon for the synthesis of amino acids in order to prevent internal accumulation of toxic compounds such as ammonia in leaf tissues. Leading on from this work, Brun et al. (2002) also found evidence of nitrogen toxicity when they exposed *Z. noltii* to a varying number of pulses of ammonium (from 1 to 8) delivering a total dose of 200 μM ammonium, which resulted in significant reductions of growth and primary production. When they validated this work in the field, they obtained comparable inhibitory affects during winter, but interestingly not in spring, which Brun et al. (2002) suggest is due to higher sucrose levels in the plants being able to meet the increased carbon demand required for N assimilation.

Other studies (Short et al., 1995; Moore and Wetzel, 2000) have not found similar responses for *Z. marina* at more ecologically relevant levels of nutrient enrichment. Moore and Wetzel (2000) suggest that differences in methods of nutrient delivery may have influenced these responses. Burkholder et al. (1992) enriched once a day with a single pulse of nitrate in a system with limited water turnover (0.05–0.1 day^{-1}), maintaining ~200–300 μM NO_3^- for the highest treatment throughout the experiment, whereas Moore and Wetzel (2000) provided a more continuous application of nutrients and higher water exchange (2–16 day^{-1}). It should also be noted that *Z. marina*, one of the species most frequently investigated, has the highest mean and widest range of nitrogen and phosphorus content of the 27 species reviewed by Duarte (1990), and consequently its nutrient requirements and tolerances to eutrophication are unlikely to be indicative of the majority of species, particularly the more nutrient sensitive species found in the Mediterranean and Australia. A greater range of species must be examined for evidence of nitrogen toxicity before it will be possible to draw any solid conclusions about the generality of this process. In the oligotrophic open waters of south and south-western Australia, there is evidence from seagrass losses in the past indicating that some species, such as *Amphibolis antarctica*, are highly sensitive to elevated nutrients (Shepherd et al., 1989). Walker and McComb (1988) demonstrated that *A. antarctica* meadows growing in Shark Bay (Western Australia) could sustain relatively high rates of production in an extremely low nutrient environment. In fact, it has been shown that *A. antarctica* leaves can take up ammonium at rates 5–38 times higher than rhizomes, in addition to having the ability for surge-uptake during pulses of very high ammonium concentrations over short (2–4 h) periods (Pedersen et al., 1997). In the absence of mechanisms to exclude or dump excess N, it is interesting to speculate that eutrophication may cause species like *A. antarctica* to quickly reach tissue N saturation and possibly toxicity, although this is yet to be investigated.

6. Sediment-Bound Nutrients

There are different tolerances and abilities for seagrasses to deal with nutrient enrichment, depending on whether the source of nutrients is delivered in the sediments or water-column and whether the sediments are predominantly carbonate or terrigenous. For instance, *Zostera marina* appears to be more susceptible to water column ammonium toxicity when grown on sand compared with mud, possibly because carbon supply is more limited on sand (van Katwijk et al., 1997). In south Sulawesi (Indonesia) mixed seagrass meadows growing on N and P rich terrigenous sediments from coastal areas (including *Thalassia hemprichii*, *Enhalus acoroides*, and *Halodule uninervis*) had higher algal biomass (phytoplankton, epiphytic algae and macroalgae), lower below-ground biomass relative to above-ground biomass, and higher tissue N and P content compared with similar seagrasses growing on carbonate sediments in reef flat environments (Erftemeijer, 1994). This work also supported the conclusions of Short (1987) that seagrasses growing on terrigenous sediments are typically N-limited, while those growing on carbonate sediments in tropical environments are generally P-limited, due to the adsorption of phosphate onto carbonate mineral surfaces. Although Udy et al. (1999) found evidence that N rather than P was the main limiting nutrient for *Halodule uninervis* and *Syringodium isoetifolium* at Green Island (Great Barrier Reef), this was possibly related to sewage from the outfall on the island which has a low N:P ratio.

Seagrasses also seem to be more tolerant of higher levels of nutrients in the sediments than the water column. Peralta et al. (2003) demonstrated a high tolerance of *Z. marina* to nutrient enrichment of pore water up to 30 mM ammonium, compared with only 25 μM ammonium (van Katwijk et al., 1997) or 200–300 μM nitrate (Burkholder et al., 1992) required in the water column to produce symptoms of nitrogen toxicity. While Van Lent et al. (1995) enriched sediments up to ~60 μM ammonium and still reported positive effects for a perennial population of *Z. marina* growing in mesotrophic lagoon waters in Grevelingen (The Netherlands) and Dennison et al. (1987) reported ammonium saturation levels for *Z. marina* growing in Great Harbor, Woods Hole, as high as 100 μM, although they did obtain a clear (but statistically non-significant) trend of decreasing root production rate with increasing sediment ammonium concentration for plants growing in shallow water and mentioned the possibility of toxic effects at high ammonium levels. Several factors have been proposed to explain why ammonium is less toxic to roots than leaves including: a lower ammonium uptake rate in the roots, lower pH of sediments compared with the water column and the release of oxygen by the roots which reduce nitrification in the surrounding rhizosphere (van Katwijk et al., 1997). However, it is important to consider that Australian and Mediterranean seagrasses have evolved in relatively nutrient poor environments, with little terrestrial runoff and these levels of tolerance to pore water enrichment may not apply in these situations.

7. Sediment Anoxia

Point sources of eutrophication such as finfish cage culture, not only add nutrients to the water column, promoting phytoplankton growth and associated light attenuation, but also contribute organic matter. When organic matter accumulates in the underlying substrate, it causes a reduction in the redox potential of the sediments leading to conditions of anoxia. It is suggested that this in turn places a greater oxygen demand on the roots and can interfere with N metabolism (Pregnall et al., 1984), as well as leading to the production of sulfide compounds which are toxic to seagrasses (Delgado et al., 1999). Sediment sulfides can diffuse through the rhizosphere directly affecting the below-ground root tissues (Erskine and Koch, 2000). High sulfide levels have also been linked to decreases in the photosynthetic capacity and efficiency of species such as *Zostera marina* (Goodman et al., 1995) and these impacts may compound the effects of other stressors to seagrass such as reduced light availability, salinity and temperature (Koch and Erskine, 2001). There has been a direct relationship found between sediment sulfide and mortality in *Thalassia testudinum* (Carlson et al., 1994), and this needs to be examined in other enriched systems. In this model, sediments enriched in organic production results in increased sulfide levels that decrease seagrass production, lead to decreased sediment sulfide re-oxidation and subsequently even higher levels of sulfide, that further decrease seagrass production.

8. Recovery

Of the relatively few studies where recovery from eutrophication has been documented, it has been reported that seagrasses take many years to recover. Not only are seagrasses notoriously slow to recolonize following a decline, particularly if seedling recruitment is the only means of re-colonization (Orth and Moore, 1986; Olesen and Sand-Jensen, 1994; Kirkman, 1997), but there may also be a significant nutrient load stored in the sediments which is available to be re-mineralized and released into the water column for years after the source of the nutrients is ameliorated. Several case studies in Australia and France following recovery after the removal or upgrade of sewage outfalls found little evidence of successful recovery of *Posidonia* spp. (Hillman et al., 1991; Pergent-Martini and Pergent, 1996; see also Walker et al., Chapter 22). Similarly, the complete loss of seagrass adjacent to a sludge outfall in South Australia described by Neverauskas (1987) was revisited 8 years after the outfall was decommissioned. This recent work revealed that seagrass cover had increased from 0 to 33% in a 2 ha study area adjacent to the outfall; however, this was comprised almost entirely of fast-growing *Halophila australis*, with only 4% cover of the original species (*Amphibolis antarctica*, *Posidonia angustifolia*, and *Posidonia sinuosa*) (Bryars and Neverauskas, 2001).

In Florida, reductions in point source nitrogen loads during the 1980s and early 1990s led to a decline in bay-wide nitrogen loads by approximately 60% in Tampa Bay (TBNEP, 1996; Johansson and Greening, 1999) and 50% in Sarasota Bay (SBNEP, 2000). In response, seagrass coverage in Tampa Bay increased by 15% between 1982 and 1999, while coverage in Sarasota Bay increased by 7% between 1988 and 1999 (Tomasko, 2002). Overall, a national survey of eutrophication in US estuaries, Bricker et al. (1999) found trends of increasing seagrass coverage in only 16 out of 138 estuaries surveyed: and noted that seagrass coverage was increasing in 2 for the North Atlantic coast, 8 for the Middle Atlantic coast, 1 for the South Atlantic coast, 4 for the Gulf of Mexico, and 1 for the Pacific coast. In contrast, seagrass coverage had declined in 49 of the 138 surveyed estuaries (36% of the total).

B. Sediments

1. Sources of Sediments

Sediments can be terrigenous or carbonate in origin, but it is generally the terrigenous sediments from human-induced perturbations that cause most of the problems via river runoff, storm water outfalls and dredging activities. This may be due, in part, to the concentration of suspended sediment derived from terrigenous sources, as well as the effects of the sediment type on light attenuation. Typically, specific light absorption or light attenuation is greater with sediment derived from organic-rich terrestrial sources than with carbonate sediments (Kirk, 1994) and wavelength specific attenuation increases with distance up the estuary (Moore et al., 1997). Carbonate sediments tend to be produced in situ from calcareous animals and epiphytic algae and may have less impact on seagrasses due to potentially higher backscatter to absorbance ratios than terrigenous sediments.

2. Process of Sedimentation and Turbidity

It is often difficult to separate the contributions of high levels of turbidity and sedimentation to seagrass decline, because sources of particulate matter, such as terrestrial runoff, industrial effluents or dredging, usually simultaneously increase both turbidity and sedimentation. Once in the system, fine sediments can be continually re-suspended and re-deposited through time (Koch, 1999). This makes it difficult to reverse the effects of elevated sedimentation, especially in a relatively closed bay or estuary as there is very little opportunity for the sediments to be flushed out of the system. The relationships between wave and current induced sediment re-suspension in shallow water areas and light attenuation are not as yet well quantified and are important areas for further work. Ward et al. (1984) found that the influence of waves on sediment re-suspension in an estuarine embayment of a system long influenced by human activity was affected by the relationship between the seagrass canopy height relative to the water depth. Suspended particulate matter concentrations were significantly lower within areas of the embayment colonized by seagrass beds. However, when water levels were elevated by spring tides or storm surges, the plants were less effective at attenuating wave energy and suspended sediment concentrations increased inside the beds. Moore (1996) observed over a range of water levels that the capacity of eelgrass beds to reduce suspended sediment concentrations within the beds decreased with decreasing plant cover in the bed. At approximately 25–50% cover there was little difference between vegetated and un-vegetated areas.

3. Turbidity

The primary detrimental effect of sediment turbidity, as with eutrophication-linked phytoplankton blooms, is the increased attenuation of light. Reduced light over prolonged periods can deplete seagrass carbon reserves or, in cases of extreme light deprivation, the lack of photosynthetically-produced oxygen can lead to sediment anoxia and more rapid mortality. Turbidity has been responsible for some very significant seagrass losses in the past, such as the massive 100,000 ha loss of seagrass during a cyclone in Hervey Bay (Queensland, Australia) and its aftermath causing widespread flooding and prolonged turbidity, where seagrasses in shallow water were uprooted in heavy seas and those below 10 m depth were thought to have died from light deprivation due to increased river runoff associated with land clearing and erosion (Preen et al., 1995). Similarly, an extensive decline of 17,890 ha of seagrass and macro-algae occurred in Western Port Bay (Victoria, Australia) during the 1970s and 1980s (Bulthuis et al., 1984a). Although the causes are not known with certainty, losses have been correlated with large volumes of terrestrial runoff, originating from extensive land clearing and soil erosion within the catchment and waterways, as well as activities such as regular dredging of shipping channels. The pattern and nature of the Western Port decline suggests an increasing exposure of the intertidal seagrass beds to desiccation due to the accretion of sediments on mudflats causing higher bed elevations, as well as directly smothering seagrasses with sediments and reducing light through persistent turbidity (Bulthuis et al., 1984a; Shepherd et al., 1989; Stephens, 1995). It is also likely that high turbidity and nutrients, associated with sediment resuspension over denuded areas, in combination with erosion from waves and tidal currents played a role in accelerating and perpetuating further seagrass losses (Bulthuis et al., 1984b; Clarke and Kirkman, 1989; Walker and McComb, 1992). Onuf (1994) found that the timing and spacing of dredging activity in Laguna Madre, Texas correlated closely with decreases in seagrass distribution. These impacts, which were long-lasting over wide areas, were not related to the sediment plumes of the initial dredging operations themselves, which were short lived but to the re-working and re-suspension of the dredged material that had been deposited in shallow areas.

4. Smothering

Very little work has been done to date investigating the effects of smothering and burial by sediments; however, it appears that tolerance is linked to sediment condition and seagrass species. For example, *Posidonia* spp. in Holdfast Bay (South Australia) survived for approximately 4 months buried under aerobic sediments compared with less than 2 weeks in anoxic sediments (Clarke, 1987) and less than a week for the more fragile *Halophila australis* (Clarke and Kirkman, 1989). However, the mechanisms of mortality were not investigated in this study, so the relative contributions of total light reduction vs. lack of gas exchange during sediment burial are not clear. Orth and Moore (1983) reported considerable dieback in submerged aquatic vegetation following a tropical storm in 1972 that deposited tremendous amounts of sediment from the catchment into the upper Chesapeake Bay burying aquatic vegetation in that region. Much of this acute impact could be related to the construction of dams above the tidal influence of the system that had filled with sediment over many decades. Not only did the freshet of water from the storm erode sediment from the catchment basin, but also huge quantities of sediments stored behind the dams were re-suspended, removed, and deposited in the estuary (Grant-Gross, et al., 1978).

Once the integrity of the meadow has been damaged (whether chemical or physical) it will be exposed to increased damage by sediment re-suspension and siltation, as seen in Western Port Bay, finally leading to auto-catalytic decline (Larkum and West, 1982). More recent work has shown that once the bottom cover of seagrass has decreased to 25–50% then re-suspension increases markedly (Moore, 1996).

5. Ecophysiology of Sediment Impacts

Both sedimentation and turbidity reduce the light available for photosynthesis and hence production of carbohydrate reserves. In this respect, the physiological effects of poor water clarity on seagrasses are the same whether the cause is increased suspended particulate matter, or eutrophication induced phytoplankton blooms, except that sedimentation and smothering have the added stress of inhibiting gas exchange. The minimum light requirements for seagrasses vary between 5 and 20% surface irradiance (Dennison et al., 1993), although it seems that the duration of time exposed to low light conditions is also important. For example, while *Halophila ovalis* appears to be able to survive for 1 month under low light conditions (Longstaff and Dennison, 1999), species with larger rhizomes and hence greater carbon storage, have managed to survive more than 5 months at minimum light requirements (Gordon et al., 1994; Lee and Dunton, 1997). Other species are much less tolerant, for example, *Z. marina* has been observed to decline after as little as 20 days of reduced light availability during summer (Moore et al., 1997). However, this could be an interactive effect of reduced light with elevated temperature. Duarte et al. (1997) predicted that mortality from burial should increase with decreasing seagrass size, but that capacity to recover should also increase with decreasing size. They tested this on a number of species in the Philippines and found that the largest species, *Enhalus acoroides*, had significant reductions in shoot density only after 10 months, while *Thalassia hemprichii* mortality increased with burial depth and most of the smaller fast-growing species showed an initial decline in deeper sediments, with some species (e.g. *Halodule uninervis*, *Syringodium isoetifolium*, and *Cymodocea serrulata*) able to recover after approximately 1 year.

Not surprisingly, the effects of turbidity on the ecophysiology of seagrasses have often been investigated indirectly through shading experiments. There have been numerous light reduction experiments done in laboratories and in situ on a wide range of seagrass species at one time or another (e.g. Dennison and Alberte, 1982; Abal et al., 1994; Short et al., 1995; Moore et al., 1997; Longstaff and Dennison, 1999; Moore and Wetzel, 2000). The most consistent conclusion regarding the effects of reduced light, and therefore implied effects of turbidity, is reduction of photosynthetic capacity, productivity and consequently the depletion of storage reserves, resulting in increasing shoot mortality and ultimately the decline of whole meadows. Burke et al. (1996) found that experimental shading of eelgrass in the spring for only 3 weeks reduced sugar concentration in the leaves, rhizomes and roots by 40–51%. Potential non-structural carbohydrate reserve (NSC) storage during shading was reduced by approximately 66%. Moore et al. (1997) found that as little as 20 days of light reduction by high springtime turbidities at eelgrass transplant sites in the same region resulted in complete loss of transplant during the summer compared to little loss in areas that did not experience the springtime light reductions but had similar summertime conditions. Such studies suggest that certain species may have critical periods for both growth and storage of NSC that enable plants to maintain positive carbon balances during subsequent stressful periods during the year.

Sediment, especially silt, can also have an impact on gas exchange, in addition to causing anoxic conditions and producing toxic sediment sulfide levels, as discussed earlier. While sulfide has been shown to negatively affect seagrass photosynthesis, metabolism, and growth (Goodman et al., 1995; Erskine and Koch, 2000; Holmer and Bondgaard, 2001), research is needed to determine whether sediment has any impact on gas exchange. If the sediment were to increase the diffusion boundary layer for gas exchange across the leaf surface, this could severely inhibit photosynthesis. This gas exchange problem would occur concurrently with reduced light penetration to the leaf surface.

6. Recovery

Very few studies have investigated recovery after a sediment-induced seagrass decline, but as mentioned earlier, once sediments are resuspended they can create a cycle of continued turbidity and sedimentation. In the case of Western Port Bay, the denuded tidal flats, where the abundance of fine silt and a regime of strong tidal currents ensured that fine sediments were continually resuspended, which were not conditions conducive to seagrass recolonization, growth and survival. Of the 12,970 ha of *Heterozostera tasmanica, Zostera muelleri*, and *Amphibolis antarctica* that were lost between 1973 and 1984 (Bulthuis and Woelkerling, 1981; Bulthuis et al., 1984a), a follow-up survey by Stephens (1995) revealed that only 3,400 ha of the affected area had recovered (less that 2% recovery per year). Most of this was recovery by *Z. muelleri* colonizing intertidal mud banks that were previously dominated by *H. tasmanica*, indicating that these beds are possibly too shallow now for *H. tasmanica* to survive increased periods of exposure to desiccation (S. Seddon, personal observation). In Hervey Bay, 2 years after the cyclone and floods, limited recovery had occurred from surviving seed stock, but only in deeper water (>10 m), whereas the lack of recovery in shallow water was attributed to the lack of viable seed surviving after the cyclone (Preen et al., 1995).

C. Herbicides

1. Sources of Herbicides

Herbicides are introduced to estuaries mainly as runoff from agricultural and municipal applications, whilst several herbicides are directly introduced as biocides on ships hulls. Recent studies of herbicide contamination in the UK and Queensland have demonstrated that herbicides accumulate around the sources and tend to be at much lower concentrations in off-shore sediments (Haynes et al., 2000a; Thomas et al., 2000). While sediment and surface water concentrations give an indication of amounts of herbicides in the environment, they give no indication of the effects on biota. More detailed studies are required in other parts of the world to fully understand the extent of herbicide contamination.

2. Processes of Herbicide Contamination

Herbicides are generally persistent compounds that, due to their chemical structure, can be resistant to microbial attack (Solomon et al., 1996). But biodegradation and photodegradation in marine environments can considerably reduce the half-life of these toxins. The most common herbicide, atrazine has a half-life of 3 days in estuarine waters (Solomon et al., 1996) and Irgarol 1051 has a half-life in seawater of 100 days (Scarlett et al., 1999). Yet degradation of a compound does not necessarily reduce the risk, for example, the degradation product of Irgarol 1051, M1, remains toxic to macrophytes and algae (Okamura et al., 2000). Models of herbicide fate predict that atrazine and Irgarol 1051 will predominantly remain in the water column, with very little material adsorbing to the sediments or entering biota (Rogers et al., 1996). This model is supported by sediment concentration data for these and other herbicides (Thomas et al., 2000). While atrazine remains in surface waters, its toxicity tends to be minimized, as it diffuses throughout the water column (Mersie et al., 2000), effectively reducing the dose in large water bodies. Nevertheless, despite the low concentration of herbicides adsorbing to sediments, concentrations of herbicides in sediments provide the best history of previous exposure (Thomas et al., 2001).

3. Status of Herbicide Contamination

Accumulation of herbicides in the marine environment has been noted in several areas around the world. In the UK, antifouling biocides such as diuron and Irgarol 1051 have been detected in sediments of a number of estuarine and coastal areas (Thomas et al., 2000; Thomas et al., 2001). Haynes et al. (2000) surveyed the concentrations of a number of herbicides in sediment and seagrass in Queensland. Diuron was the substance of most concern, occurring at concentrations that may affect seagrasses. However, the relationship between contamination and resulting impacts needs to be more fully investigated. For example, concentrations of triazine and polyurea herbicides in Wadden Sea sediments showed a connection to seagrass condition (Bester, 2000), yet the concentrations of other contaminants such as metals were not considered, so causality has not been fully demonstrated. Investigation of herbicide contamination is limited to a few regions.

Studies in Asia and the Mediterranean need to be conducted to gain a better understanding of global trends.

4. Ecophysiology of Herbicides

Research into indirect impacts and level of contamination from agricultural herbicides over the past 30 years has covered a wide range of compounds and seagrass species. Recent application of antifoulant-herbicides has included the use of Irgarol 1051 and Diuron (Thomas et al., 2000); however, limited research has been directed at understanding the impact of these compounds on non-target organisms, such as seagrasses (Leadbitter et al., 1999; Scarlett et al., 1999; Ralph, 2000). Herbicides move readily into seagrass tissue, and uptake of atrazine has been shown to occur through both the leaves and roots (Schwarzschild et al., 1994). The effect on seagrass is greatly reduced when the uptake pathway is via the roots, similar to nitrogen toxicity as discussed in the previous section. The impact sites of most common herbicides are well documented for target species, and are likely to be identical for seagrasses. For example, diuron reversibly inhibits photosynthetic electron flow to plastoquinone in photosystem II (PSII) by blocking the electron transport chain after the primary electron acceptor (Q_A) (Miles, 1991), with similar effects shown for atrazine (Solomon et al., 1996).

Despite the widely acknowledged risk of herbicide contamination, toxicity testing using estuarine plants remains in its infancy (Lytle and Lytle, 2001). Thus, there is only limited data available on the sensitivities of different species to determine critical levels of toxicants for the conservation of these ecosystems. For example, diuron at 10 μg L^{-1} was shown to reduce effective quantum yield of photosynthesis by approximately 50%, however these levels only occur during storm events, when the seagrass will be exposed to the additional impact of freshwater stress and increased turbidity. These environmentally relevant interactions are presently unknown, and we may be underestimating the impact of such pollution events (Haynes et al., 2000b).

Not all seagrasses respond to herbicides to the same degree and a comparison of diuron effects on three seagrass species by Haynes et al. (2000b) demonstrated variation in effective quantum yield responses. *Halophila ovalis* appeared more sensitive to lower concentrations of diuron than *Zostera capricorni* and *Cymodocea serrulata*, which may have implications for the long-term composition of a mixed meadow. Competitive fitness of one seagrass species may result in the change of the community structure, as one species suffers a substantial decline, changing the trophic interactions based on that meadow (El Jay et al., 1997). To further understand the impact on community scale processes, we also need to understand whether particular life-stages are more sensitive than others, such as seedlings, meristematic tissue, and mature leaves.

5. Bioaccumulation of Herbicides

Seagrasses have been found to bioaccumulate herbicides, which creates problems throughout associated food webs. The capacity of the seagrass to bioaccumulate a toxic compound will define its trophic threat. For example, irgarol can be accumulated at up to 25,000 times the background level (<0.003 µg dm^{-3}) in *Z. marina* (Scarlett, 1999). Irgarol does not appear to depurate in fresh seawater. This suggests that the herbicide burden will accumulate during periods of elevated contaminant load, but will not diffuse back out of the seagrass when flushed with clean water. Therefore, herbicides would be available for consumption by grazers such as dugongs, which in fact have been found to have elevated levels of herbicides (Haynes et al., 2000a). This is in contrast to the rapid recovery of *Z. capricorni* after in situ exposure to irgarol, diuron and atrazine on return to uncontaminated water (Macinnis-Ng and Ralph, 2003a), a characteristic of PSII inhibitor herbicide impact on aquatic macrophytes (Bowmer, 1986). Further investigations of detoxification processes may address this anomaly between acclimation and physiological responses.

Genotypic and phenotypic plasticity is a common phenomenon within seagrass populations (Waycott, 1998; Waycott et al., Chapter 2). Site-specific variation in herbicide tolerance means extrapolation of sensitivity/tolerance data should be treated cautiously. For example, Macinnis-Ng and Ralph (2003a) found that diuron toxicity to *Z. capricorni* was more toxic both in situ and in the laboratory, than Haynes et al. (2000b) found for the same species occurring 1000 km north. A 5-day exposure period for the plants from the northern site showed effective quantum yield ($\Delta F/Fm\prime$) of around 0.2, whereas those from the southern population showed values of 0.0 after only a few hours of exposure. These regional differences could be indicative of chronic sub-lethal acclimation, or that the plants from the southern site were less tolerant. This suggests that tolerance is not constant within a species across a wide geographic distance and that local microenvironment strongly influences the tolerance.

6. Recovery from Herbicides

Few seagrass studies have seriously considered recovery from chronic exposure to herbicides. Recovery from acute herbicide exposure is a common response for macrophytes (including seagrasses), but this needs to be considered from a more ecological perspective. Bowmer (1986) demonstrated that the PSII inhibitory effect of herbicides (such as diuron and atrazine) on macrophytes was reversed once the contaminant was removed, and photosynthesis rapidly recovered. This aspect of herbicide toxicology is rarely considered in laboratory experiments and is a critical consideration in the interpretation of any field based herbicide exposure experiment. Haynes et al. (2000b) found three species of seagrass recovered when returned to fresh seawater after 5-days exposure to diuron. While Macinnis-Ng and Ralph (2003a) found a virtual halt in photosynthetic activity induced by exposure to atrazine, irgarol and diuron was reversed on return to fresh seawater in the laboratory and field. The exposure period was only 10 h and it is not known if the seagrass would recover after a longer exposure period. Field conditions would typically resemble a single pulse of contaminant, followed by a period of flushing, followed by a subsequent pulse of contaminant (Solomon et al., 1996), and experiments are needed which simulate this effect.

Assessing endpoints such as growth may represent a more ecologically relevant outcome, but it may not be the most sensitive indicator of stress, as the plant has a longer period of time for phytoremediating processes to detoxify or adapt to the contaminant. Conversely, a more sensitive endpoint may illustrate an impact, which could possibly be reversed by returning the plant to un-contaminated water. For example, *Z. marina* exposed to 5–10 μg L^{-1} atrazine for 5 weeks significantly reduced growth (Schwarzschild et al., 1994), whereas *Z. capricorni* after just 10 h exposure showed a significant impact on PSII photochemical efficiency, although this impact was completely reversible in situ (Macinnis-Ng and Ralph, 2003a). This clearly demonstrates the different sensitivities of these two partially related endpoints.

D. Heavy Metals

1. Sources of Heavy Metals

Heavy metals can enter the marine environment naturally via weathering and erosion of rocks and soils (Batley, 1996) or through urban and municipal runoff, storm water, sewage, industrial effluents, mining operations, atmospheric deposition and agricultural activity (Batley, 1996; Irvine and Birch, 1998; Haynes and Johnson, 2000). In addition, activities such as dredging can release heavy metal-laden sediment from anoxic deeper layers allowing metals to be re-mobilized and available to contaminate the biota (Batley, 1987; Lytle and Lytle, 2001).

2. Processes of Heavy Metal Contamination

Bio-availability of heavy metals is influenced by water and sediment pH, sediment particle size, redox potential, dissolved organic matter, sediment cation exchange capacity, water temperature, salinity, organic content, and the concentrations of other metals (Batley, 1987; Ward, 1989; Batley et al., 1999; Alutoin et al., 2001). These physicochemical parameters influence processes that affect heavy metal availability, such as chelation, complexing, precipitation, absorption, and adsorption (Batley, 1987). For this reason, as well as the more complex nature of the field environment, heavy metals are less bio-available and generally have a less toxic effect in the field that the laboratory (Graney et al., 1995), thus extrapolating laboratory findings to the field can be unreliable. This is confirmed by recent comparisons between laboratory and field assessments of toxic metal impacts on photosynthesis, suggesting that laboratory experiments may overestimate metal effects (Macinnis-Ng and Ralph, 2002).

The main difficulty with understanding metal impacts on seagrasses is quantifying the exposure, as it is transient and highly variable in its distribution between water, sediment, seagrass and epiphytes. It is important to establish how much heavy metal is really available in the water column to be absorbed by the seagrass (Haynes et al., 2000a). Due to the complex nature of seawater, many compounds have limited bio-availability. Consequently, much of the contaminant load is not available to the seagrass. Simply measuring concentrations of metals in sediment or water will not accurately indicate the impact, because the physicochemical conditions in a particular habitat will determine the bio-available fraction. There may be high concentrations of metal in the sediment, but if the material is bound to the sediment, it may not have a toxic impact on biota. Variation in sediment conditions outlined above can change how metals are bound and thus, a site with low concentrations of metals in sediment may indicate low binding ability, as much as low contamination. Relating environmental concentrations to concentrations in tissues (and therefore impact levels) is problematic due to the variability in accumulation phenomena, as outlined below.

Pergent-Martini and Pergent (2000) have pursued the question of metal accumulation in seagrasses for many years, providing a detailed understanding of the distribution and some mechanisms of metal uptake. They found accumulation varies according to the specific heavy metal, the species of seagrass being assessed, the tissue-type (including compartment, and age), the sampling period and the level of contamination. Thus, assessing the abundance and distribution of metals in seagrass meadows is relatively straightforward, but determining the source, uptake and impact of these metals requires more research. Heavy metal uptake is widely believed to be controlled by exposure concentration, which is a passive, surface area-dependent process (Ward, 1989; Malea et al., 1995). Heavy metal uptake into a seagrass can follow two pathways: from surrounding water to leaves then rhizomes or acropetal translocation from interstitial water (in the sediment) into roots to rhizomes and leaves. Very little is known about the cellular uptake mechanisms, toxicology, and heavy metal acclimation in seagrasses.

Uptake of heavy metal contaminants also appears to be influenced by season. This has been previously attributed to variations in growth rates that dilute the accumulated metals (Lyngby and Brix, 1982); however, new evidence suggests that climatic patterns show an equal or greater influence on the seasonality of metal accumulation. Prange and Dennison (2000) found the seasonal changes in concentration were associated with seasonal rainfall events, leading to changes in metal load in the water/sediment. Schlacher-Hoenlinger and Schlacher (1998) suggested that storm frequency and seasonal rainfall influence heavy metal accumulation, in conjunction with the annual growth cycle. Seasonal weather patterns are also linked to sediment re-suspension and microbial degradation of heavy metals.

As noted earlier, toxicity testing using estuarine plants is a relatively new area of research (Lytle and Lytle, 2001). Thus, there is only limited data on the sensitivities of different species and there is sparse data available for determining critical levels of toxic metals for the conservation of these ecosystems. For example, two species of *Halophila* were found to be impacted by iron and copper exposure, while *Zostera capricorni* was only affected by copper and *Halodule uninervis* and *Cymodocea serrulata* remained unaffected (Prange and Dennison, 2000). More studies that compare a number of species are required to fully understand metal effects on different taxa, as opposed to measuring metal accumulation.

3. Status of Heavy Metal Contamination

Heavy metal contamination in estuarine areas has been identified across the world. Mediterranean studies were reviewed by Pergent-Martini and Pergent (2000) and this seems to be the area with the most information available in the literature. There are some Australian studies such as Fabris et al. (1982), Batley (1987), Ward (1987), and Prange and Dennison (2000).

4. Ecophysiology of Heavy Metals Impact on Seagrass

Most of the heavy metal research has focused on the accumulation of metals into seagrasses (Sanchiz et al., 2001). Seagrasses are good as biomonitors, as their tissue metal content often reflects bio-available water/sediment content (Sanchiz et al., 2001), but this is not true for all species for all metals. Few studies have considered the physiological impact of the metals on the seagrass (Ralph and Burchett, 1998a; Prange and Dennison, 2000; Macinnis-Ng and Ralph, 2002). Understanding the ecophysiology will allow us to understand the role of contaminant metals in the marine environment, not simply identify the presence and location of the contaminants. Since ample evidence has been collected over the past years to show that seagrasses accumulate heavy metals, we now need to understand whether metals can kill, permanently damage or merely cause stress to the seagrass. From a management perspective we also need to know which species are able to accumulate/concentrate which metals.

Different populations of the same species within a small geographic distribution can have widely different tolerances to metal impacts. Three in situ populations of *Zostera capricorni* within 80 km in the Sydney region exposed to copper showed different declines in photosynthetic efficiency (Macinnis-Ng and Ralph, 2004). It is not clear whether this was due to genotypic or phenotypic variation between the populations. Organisms can become resistant to pollution either through acquiring tolerance as individuals via physiological adaptation or through genetically based resistance, which renders a population resistant (Klerks and Weis, 1987). Background levels of metals in the sediment, water column, and seagrass did not correlate with the different metal impacts and the mechanisms of tolerance remain unclear. Further investigations of interactions between metals and other stress factors (e.g. eutrophication and turbidity) are needed, as well as understanding the process of compartmentalization of metals within the tissue, since tolerant populations may have the ability to isolate certain metals, reducing the toxic impacts (Pergent-Martini and Pergent, 2000).

It is important to consider why different physiological endpoints show different degrees of sensitivity. Heavy metals have a number of impact sites on the photosynthetic apparatus; these include thylakoid membrane stability, photophosphorylation, inhibition of chlorophyll synthesis, blocking electron transport or inhibition of the Calvin Cycle enzymes (Clijsters et al., 1999). The effect of different impact sites can be seen in the growth rate of *Z. capricorni* being reduced by 10 mg L^{-1} of copper, cadmium, lead, and zinc after a 10 day exposure period, while changes in photosynthetic rate (measured as O_2 production) were less pronounced (Conroy et al., 1991). Thus, endpoint selection can influence the perceived threat of a particular contaminant but a good understanding of mechanisms of toxicity can minimize this problem.

Detoxification is also an important aspect of tolerating contaminants. Generation of active oxygen species is an important part of metal toxicity. To avoid accumulation of these toxic intermediates, plant tissues have a series of detoxifying agents that involve enzymatic and non-enzymatic mechanisms (Clijsters et al., 1999). An absorbed pollutant compound has one of three fates within an organism (Pergent-Martini and Pergent, 2000). It can be trapped in a neutral fraction and stored in a compartment of the organism, it can find its way to a fixation site or it can be metabolized by biotransformation enzymes. Exposure to metals generally stimulates enzyme activity (Clijsters et al., 1999), since natural elimination of toxic substances is encouraged by biotransformation enzymes increasing their water solubility (Pergent-Martini and Pergent, 2000). This process involves oxidation of the pollutant, followed by binding with glucuronic acid, glutathione, sulfates or water molecules. The bioavailability of pollutants is decreased when they are metabolized by the P450 or peroxidase systems and incorporated into the lignin of the plant cell wall (Pergent-Martini and Pergent, 2000). Peroxidase activity has been found to increase with the onset of metal toxicity as a detoxifying mechanism (MacFarlane and Burchett, 2001).

5. Recovery from Heavy Metal Exposure

Heavy metals generally disrupt the function of photosynthesis; however, permanent damage may not be caused, since the impact can be reversed by the removal of the metals such as cadmium, copper and lead (Prasad and Strzalka, 1999). Therefore, recovery is possible, and acclimation to chronic metal contamination has been documented (Ward, 1987). For example, Prange and Dennison (2000) were able to demonstrate recovery of *Z. capricorni* after exposure to copper, once the Cu-laden water was removed, the photosynthesis recovered. These types of toxicity-based investigations provide an ecological perspective of the impact of metals. The potential for recovery from heavy metal exposure is as important as understanding of the degree of damage caused by exposure.

Metal-binding polypeptides (phytochelatins) are another mechanism employed to confer metal tolerance. Phytochelatins reduce the concentration of toxic free metal ions by binding in the cytoplasm (Verkleij and Schat, 1990; Turner, 1994). The influence of phytochelatins on tolerance is thought to be minimal since there is little evidence of quantitative differences between the rate and capacity of phytochelatin production between sensitive and tolerant plants (Verkleij and Schat, 1990). However, these detoxification processes that promote recovery have not been fully investigated in seagrasses.

E. Petrochemicals

1. Sources of Petrochemicals

Petrochemicals are introduced into the marine environment as a result of hazardous materials disposal, leakage from oil storage facilities, activities in refineries, ports and harbors, and in stormwater runoff (Thorhaug, 1992). Since seagrasses are commonly found along the coastal fringe, they are always under threat from oil spills. Many large oil spills have been carefully monitored for long-term impacts on seagrasses, such as the *Exxon Valdez* and the ‘first’ Gulf War (Burns et al., 1993; Dean et al., 1998) and have shown few lasting impacts. Dispersants used to clean up spills can also pose a threat to seagrass both alone and in combination with the oil. Dispersants encourage the oil to spread and increase the bioavailable fraction of oil by increasing the concentration of petroleum-derived hydrocarbons in the water column and altering the interaction of these compounds with biological membranes (Wolfe et al., 1998).

2. Process of Petrochemicals Contamination

Generally, when seagrasses are exposed to petrochemicals, sub-lethal quantities are incorporated into the tissue, causing a reduction in tolerance to other stress factors (Zieman et al., 1984). Smothering of seagrass occurs when oil is stranded on areas of intertidal seagrass, leading to reduced growth rates, blackened leaves and mortality (Howard et al., 1989). This is only a problem for intertidal seagrasses. Oil appears to mainly affect flowering, and if plants are able to spread through apical meristem growth, flowering impacts are not a significant problem over the medium term for a well-established meadow (Dean et al., 1998). The *Exxon Valdez* oil spill in 1989 caused seagrass blades below oiled beaches to be bleached white and ultimately killed (Juday and Foster, 1990). Another study of this spill noted a decrease in the density of leaves and flowering shoots of *Z. marina* after the event (Dean et al., 1998). Dispersants consist of a surfactant in a carrier or solvent (Hatcher and Larkum, 1982). Dispersants can be toxic in their own right, but the solvent can also encourage the breakdown of the waxy cuticle, allowing greater penetration of oils into seagrass leaves and increasing phytotoxicity.

3. Status of Petrochemicals Contamination

Investigations of recent spills (*Exxon Valdez*; Dean et al., 1998) have found no overall impact on seagrass biomass, density, flowering, or seed production 1 year after the spill. No difference was found between oiled and reference sites. Similarly, as a result of the Gulf War (1991) vast areas of the coastline of Saudi Arabia were heavily oiled; however, one year after the initial event, the productivity of oiled and un-oiled seagrass meadows were the same (Burns et al., 1993). These are typical results for oil spills and reflect the general lack of field data to support any substantial long-term impact of petrochemical contamination.

4. Ecophysiology of Petrochemicals Impact on Seagrass

The primary phytotoxic effect of oil is induced by the absorption of the water-soluble fraction (WSF). The toxic components of petrochemicals are thought to be the poly-aromatic hydrocarbons (PAH), which are lipophilic, so they are able to pass through lipid membranes and tend to accumulate in the thylakoid membranes of the chloroplasts (Ren et al., 1994). Thorhaug et al. (1986) found that dispersed oil had a greater effect on the growth of *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudium* than oil alone. Similarly, Hatcher and Larkum (1982) found that stress levels in *Posidonia australis* were more severe when the oil was dispersed, in comparison to oil alone. Ralph and Burchett (1998b) found that oil + dispersant had an initial impact on effective quantum yield ($\Delta F/Fm\prime$) in *Halophila ovalis,* but some recovery occurred after 96 hours of constant exposure to the mixture. There are also examples of an oil + dispersant mixture being less toxic than oil or dispersant alone (Macinnis-Ng and Ralph, 2003b).

It is difficult to compare results from studies testing different oils and dispersants on different species (Hatcher and Larkum, 1982; Thorhaug et al., 1986; Thorhaug, 1988; Thorhaug, 1992; Ralph and Burchett, 1998b). Any one of these variables could be solely responsible for the variations in the results, or a complex interaction of the three factors could be involved. Further controlled experiments are needed to understand this complex interaction.

5. Recovery from Petrochemical Exposure

It seems laboratory experiments portray the impact of PAHs to be much more serious than field-based experiments or actual spills. There are numerous examples of oil spills having no significant impact on the seagrasses after several years. One year after the Gulf War oil spill, leaf morphology and growth indicators suggested three species of seagrass remained in good health (Kenworthy et al., 1993). Dean et al. (1998) found that *Z. marina* showed little detrimental effects 1 year after the *Exxon Valdez* oil spill. These types of impact assessments are usually based on comparing the impacted site to a reference site, as the region is rarely surveyed before the spill. This limits the scope of interpretation of this style of investigation. However, recovery of deeper seagrasses exposed to the WSF alone is generally much more successful than recovery of smothered intertidal seagrasses.

III. Management of Anthropogenic Pollutants

Information on safe pollutant loads is urgently needed for coastal resource managers to make sound decisions. Peters et al. (1997) recommend that benchmarks for risk assessment, baseline monitoring criteria and effective management strategies are needed to protect seagrasses. In this way, managers need to be able to access and synthesize information on contaminants and stressors, to predict risk to the ecosystem. To predict risk they must know the magnitude of the stressors for which a detrimental effect can be monitored. We need to provide an indication of the levels of tolerance (ideally under in situ conditions) and indicate the ecological consequences (death, reduce photosynthesis, biochemical damage) of the exposure to a known contaminant. Much of this type of data is slowly becoming available; however, it may not be in a form that is readily accessible for synthesis into risk assessment protocols.

Due to the complex nature of seagrass decline, it is rare to find clear examples of causality, and therefore it is difficult to have direct evidence of the impact of contamination on seagrass health (Bester, 2000). Additionally, in many coastal systems the stressors co-vary (Moore et al., 1996). This suggests that a comprehensive approach to management is needed, where all potential contaminants are addressed. In many cases the solutions proposed may address more than one factor. For example, improving catchment basin retention of sediment runoff will help to improve water clarity through reductions in suspended sediments as well as reducing a significant proportion of nutrient inputs.

A. Construction of Pollutant Loading Models

In response to demands of resource managers, numerical models are needed to assess the susceptibility of seagrass to nutrient enrichment and other contaminants. For example, nutrient loading models have been developed to determine the sources and quantities of nutrients coming into estuarine and nearshore marine ecosystems. Numerous studies have shown that most estuaries are strongly nitrogen limited, although in some locations, such as eastern and central portions of Florida Bay (Florida, USA; Fourqurean et al., 1992) or Shark Bay (Western Australia; Smith and Atkinson, 1983), available evidence suggests that phosphorus is the principal nutrient limiting primary production. As a result, nutrient loading models typically focus on nitrogen as the nutrient of concern.

A variety of techniques exist for determining the sources and quantities of pollutants entering estuarine and nearshore marine ecosystems. These efforts range from complex models that examine rainfall, land use, soil types, elevation changes, etc. to simple spreadsheet-type models that predict pollutant loads as a function of land use categories alone. For many estuaries, a significant percentage of the watershed is gauged for stream flow measurements. If water quality data are collected at gauge locations, then direct estimates of pollutant loads can be made (flow x concentration = load).

In many coastal ecosystems (e.g. Tampa Bay, Florida, USA; Chesapeake Bay, USA) significant point sources of nutrients from wastewater treatment plants and/or industrial facilities occur downstream of any stream flow gauge locations. Often, point sources discharge directly into estuarine waters, or into the lower tidal reaches of tributaries to these estuaries. Consequently, development of pollutant loading estimates requires knowledge of the quantity of water discharged from all relevant point sources, as well as information on the quality of the discharged effluent.

Quantification of atmospheric loads of nutrients into estuarine and/or nearshore marine waters require, at a minimum, information on the quantity and quality of rainfall. By knowing the area of open water, and the amount of precipitation that falls upon the water, the quantity of water deposited onto the open waters of the ecosystem can be determined. If the concentration of nutrients in rainfall is known, estimates can be made of the amount of nutrients delivered to the open waters of the system via direct precipitation (e.g. Tomasko et al., 2001). However, the above-described technique does not take into account the impact of 'dry' deposition of pollutant loads (i.e. atmospheric deposition fluxes not associated with precipitation).

Alexander et al. (2001) presented results of an empirical modeling effort that estimates both the direct and indirect (i.e. via stormwater runoff) impacts of atmospheric deposition of total nitrogen to estuarine and nearshore marine waters of the USA. When direct atmospheric deposition onto open waters is excluded, indirect impacts of atmospheric deposition of total nitrogen accounts for between 4 and 35% of the nitrogen load to 42 US estuaries studied, with a mean value of 20% (Alexander et al., 2001).

The implications of estimating the 'indirect' impact of atmospheric deposition vary between the estuaries examined. For example, direct wet and dry deposition of nitrogen onto the open waters of Narragansett Bay (Rhode Island, USA) was estimated to contribute 4.6% of the total nitrogen load to this system (Nixon et al., 1995). However, Alexander et al. (2001) estimate that 10% of the non-direct atmospheric load (i.e. stormwater runoff, point sources, baseflow, etc.) is due to indirect impacts from wet and dry deposition onto the watershed. Combined, the total impact of both direct and indirect deposition of atmospheric nitrogen would equal approximately 14.1% of the total nitrogen load (i.e. $4.6\% + 0.10 \times 95.4\%$). Additionally, Alexander et al. (2001) estimated that 19% of non-direct atmospheric loads to Barnegat Bay were atmospherically derived, so that 53.3% of the total load would be derived either directly or indirectly from atmospheric deposition (i.e. $42.3\% + 0.19 \times 57.7\%$).

In general, estuaries with relatively small watersheds, as compared to the amount of open water of the estuary, are more strongly influenced by direct atmospheric deposition of pollutants such as nitrogen. However, the proportion of non-point source loads (i.e. stormwater runoff) due to atmospheric deposition of pollutants onto the watershed varies as a function of land use, air quality, and stream characteristics (Alexander et al., 2001). Estuaries in the Northeastern and Mid-Atlantic portions of the US had the highest percentage of total nitrogen loads attributed to indirect impacts of atmospheric deposition onto the watershed (Alexander et al., 2001).

B. Pollutant Loads and Pollutant Yields

Nitrogen loads to estuarine and/or nearshore marine waters, minus the contribution from direct atmospheric deposition onto the open water, can be used to compare the relative pollutant loads of various portions of the contributing watershed. Nitrogen yields for Southwest Florida (USA) estuaries vary from a low value of 2.6 kg Total Nitrogen (TN) ha^{-1} $year^{-1}$ in Charlotte Harbor (Squires et al., 1998) to 10.9 kg TN ha^{-1} $year^{-1}$ in Sarasota Bay (Heyl, 1992). For estuaries in Southwest Florida, the degree of 'urbanization' of an estuary's watershed accounts for the majority of the variation in nitrogen yields (Tomasko, 2000). Similarly, Howarth et al. (1996) found nitrogen yields from both large rivers and small coastal watersheds discharging into the Atlantic Ocean were positively correlated with human population density. The amount of variation found in this correlation can be further reduced by examining land use patterns within various watersheds, as per capita total nitrogen loads are positively correlated with the percent of the watershed used as harvestable cropland (Turner et al., 2001).

Based on the above-described relationship between human population density and watershed-level nitrogen yields, it is possible to estimate a 'natural' watershed-level nitrogen yield, by deriving the yield associated with an undisturbed watershed (i.e. the calculated yield when human population equals zero). Turner et al. (2001), using a data set derived from 27 US estuaries, estimated that a natural nitrogen yield would be 1.08 kg TN $ha^{-1}year^{-1}$. If the percent of the watershed that is urbanized is plotted against watershed nitrogen yields for estuaries in Southwest Florida (e.g. Tomasko, 2000), the calculated natural watershed nitrogen yield comes out to 1.31 kg TN ha^{-1} $year^{-1}$. Estimates of natural watershed nitrogen yields derived by Howarth et al. (1996) and Nixon (1997) ranged between 0.76 and 1.10 kg TN ha^{-1} $year^{-1}$. While such estimates must be viewed with an appropriate degree of caution, they nonetheless can help to put into perspective the degree of nutrient enrichment experienced by seagrass communities in estuarine and nearshore marine environments. Thus, estimated nitrogen yields from the watersheds of the Chesapeake Bay, USA (23.4 kg TN ha^{-1} $year^{-1}$; Boynton et al., 1995), Narragansett Bay, Rhode Island, USA (18.6 kg TN ha^{-1} $year^{-1}$, Nixon et al., 1995) and Delaware Bay, USA (15.1 kg TN ha^{-1} $year^{-1}$, Nixon et al., 1996) would all appear to be substantially higher than baseline conditions.

C. Implications for Future Population Growth

As an example drawn from one of several documented cases of recovering ecosystems, seagrass coverage in Southwest Florida's estuaries has increased in recent years, mostly as a result of improvements in water quality that are, in turn, related to massive (and expensive) reductions in point source nitrogen loads (Kurz et al., 1999; Tomasko, 2002). Seagrass cover in Tampa Bay is estimated to have increased by approximately 25% between 1982 and 1996, while Sarasota Bay's cover has increased 19% between 1988 and 1996 (Tomasko, 2002). Charlotte Harbor's increase has been more moderate, a 6% increase between 1982 and 1996, and may be simply natural variability (Tomasko and Hall, 1999). Lemon Bay's coverage appears to have slightly decreased between 1988 and 1996 (Kurz et al., 1999).

Within the past 20 or so years, estuaries in Southwest Florida have experienced the combination of increased watershed population density and yet nearly simultaneous improvements in both water quality and seagrass cover. This situation has been possible mostly due to three phenomena: (1) estuaries such as Tampa Bay and Sarasota Bay had been allowed to significantly degrade by the late 1970s and early 1980s, (2) point sources of pollution (e.g. wastewater treatment plants, industrial discharges) were substantial impacts, and (3) the technology existed to reduce the loads from these point sources. Given this situation, the public might be forgiven for believing that future population growth can be accommodated without further degradation of nearshore waters and habitats.

However, the possibility exists that the relationship between nitrogen yields and the degree of urbanization of the watershed evident when comparing estuaries against each other also holds true when comparing single systems over time. That is, it is possible that comparing different systems against each other is a useful 'space for time' substitution to predict what might happen for a single ecosystem over the years. If that is true, then recent increases in seagrass coverage in Southwest Florida's estuaries (or any other locations that follow a similar pattern) might potentially be offset in the future by increased nitrogen loads associated with continued population growth in their watersheds.

IV. Recommended Research Directions

Part of the process of reviewing the current knowledge of impacts of eutrophication, sediments and contaminants on seagrasses, is to identify gaps in our understanding and recommend future research directions. In the following paragraphs we have described a series of topics where we feel research effort would be best applied.

The physicochemical conditions established with a laboratory-based exposure chamber (aquarium or mesocosm) do not replicate the in situ ecosystem. Clearly, field based assessments will be closer to reality and generally may show increased tolerance to pollutants. This increased tolerance is not linked to the plants per se; it is more likely the capacity of the undisturbed ecosystem to ameliorate the toxicants. For example, the microbial assemblage in a laboratory-based experiment bears limited resemblance to the complex system supported in situ. The interaction of sediment, microbial, fauna activities, and water quality influences on availability of toxicants is not replicated in laboratory trials. It is clearly recognized that little understanding exists to explain the complex process involved with field conditions, in comparison to the relative wealth of information derived from controlled laboratory investigations.

Assessing pollutant impacts in a toxicological approach will provide a better understanding of the risks posed by pollution to seagrass survival. Dose response is a complex interaction of concentration and exposure period; therefore short-term high dose experiments do not provide a true indication of the plant's tolerance to these contaminants. It is important that dose-response experiments are performed on a range of contaminants that are environmentally relevant. It is relatively easy to expose a plant with a toxic dose of pollutant, but if the endpoint is not sufficiently sensitive to detect an environmentally realistic dose, the outcome is merely an example of another dose that 'can' kill a seagrass; however, it is unlikely that actual exposure will be sufficiently concentrated to reach this endpoint. This is why we must be looking for the most sensitive endpoint using environmentally realistic doses.

Similarly, the frequency and duration of exposure to various contaminants deserves some attention. For example, experimental regimes simulating chronic exposure to one stressor (e.g. high turbidity) followed by a series of pulse events with assorted contaminants (e.g. herbicides and heavy metals) would be informative. Many studies showed seasonal differences in the various responses measured, so determining whether such scenarios affect seagrass health and survival more during summer or winter conditions is also important.

There is a definite need to assess a wider range of species (specifically from low nutrient environments) to nutrient enhancement and toxicity. This should include chronic low level and acute pulse exposures. In addition, more work needs to be done on the mechanisms of nutrient metabolism, exclusion and uptake, as well as methods to reduce nutrient toxicity in seagrasses.

Incorporation of the interactive stress of environmental factors (like temperature, salinity, and light) is needed to evaluate the relative contributions of contaminants, freshwater, and turbidity following storm events. More research is required on the specific mechanisms of mortality in response to sedimentation, including the relative contributions of blocking light and inhibition of gas exchange toward burial stress and eventual mortality.

Recovery is rarely considered. Equally important is the lack of data on chronic and sub-lethal impacts, as most of the literature deals with acute toxicity. As indicated in most of the sections, we are currently unaware of the impact of pre-exposure, interaction of factors (Bowmer, 1986), multiple pulses or co-tolerance.

Genetic and population influence on contaminant tolerance has not been fully investigated. Chronic low-level exposure may influence genetic selection for more tolerant genotypes or encourage enhanced phenotypic tolerance. Several studies have shown spatial separation of a species results in differences in tolerance to contaminants, and this could be linked to subtle genetic differences. Recent developments in molecular biology mean that we will soon see a range of genetic biomarkers available for identifying proteins that are damaged by anthropogenic contaminants.

V. Summary

This chapter has reviewed the role of anthropogenic pollutants in past extensive declines of seagrasses. With increasing awareness of the sensitivity of seagrasses to many pollutants, it appears that effective management of catchment processes can facilitate seagrass recovery. Some factors are well known, as are many of the important processes, while many others remain poorly understood. Yet even the well-researched contaminants (such as metals) do not have adequate safe-level guidelines for decision-makers. The culture of determining threshold levels and performing toxicological tests has not yet been applied to seagrass management, but this may be an effective route to take. Furthermore, we need to move our knowledge from the laboratory into the field, to provide data for models to predict the impact of realistic contaminant loads, and we need to test the generality of these results across a wider range of species in temperate and tropical environments. The interactive effects of different anthropogenic stressors as well as their interaction with natural stressors such as temperature and salinity are not well understood and should be the focus of research efforts. Sediment impacts on seagrass are being increasingly observed in many systems. Management efforts to control sediment inputs can potentially have a variety of positive effects on seagrass systems, because non-point source inputs of nutrients and other contaminants will potentially also be reduced.

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Chapter 25

Seagrass Conservation Biology: An Interdisciplinary Science for Protection of the Seagrass Biome

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"Planet Earth is one ocean and a bunch of islands" Harry Recher 2000. Pacific Conservation Biology V:240.

I. Introduction

A. Conservation Biology

In the past three decades seagrass research has adopted several disciplines and matured into a global science. One of the approaches we can use to focus our science to benefit the management and protection of seagrass is that of Conservation Biology; a proactive field of science bringing together academic, government, and nongovernmental organizations from a wide range of disciplines to understand and conserve biodiversity. This relatively recent field synthesises and directs insights from many disciplines for direct application to the protection and conservation of species, communities, and biomes (Fig. 1). While the primary focus for conservation biology comes from ecology, genetics, landscape ecology, population biology and taxonomy, the discipline also incorporates analytical procedures associated with the social sciences, biogeography, and evolutionary biology (Soule and Wilcox, 1980; Soule, 1985; Meffe and Carroll, 1994; Primack, 2000). Conservation biology recognizes that humans derive both extractive and intrinsic benefit from the natural world and embraces methods and analyses utilized in fisheries science, agriculture, anthropology, economics, law, philosophy, and sociology. Today, unlike traditional approaches that were rooted in the preservation and management of selected species, conservation biologists are advising natural resource managers to focus more on an ecosystem approach that includes entire biomes, and to recognize that public trust demands comprehensive protection of biodiversity as much as sustaining the yield of harvestable organisms. Conservation biology endeavors to maintain and protect biodiversity at all spatial scales, including a variety of little understood and often overlooked life forms. In the broader meaning of biodiversity we are interested in conserving ecological services as much as life forms (sensu Randall, 1986).

A. W. D. Larkum et al. (eds.), Seagrasses: Biology, Ecology and Conservation, pp. 595–623.

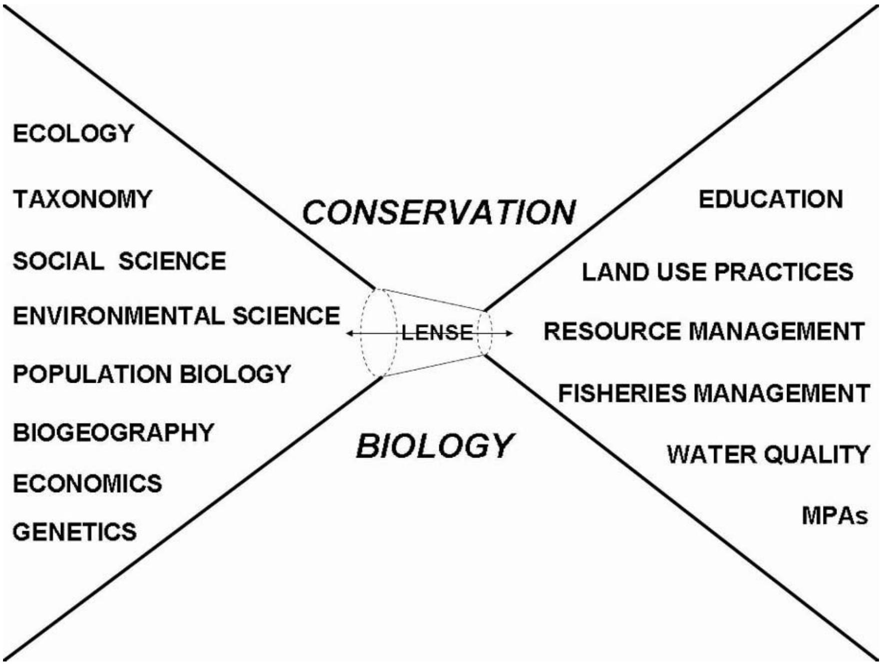

Fig. 1. This conceptual diagram illustrates the relationship between basic science (on the left) and resource management (on the right). Conservation biology serves as a lense to focus basic science for use in protection and management of natural resources and biodiversity (after Primack, 2000).

To protect biodiversity it has been suggested that conservation science be divided into four general areas: (1) identify the threats to biological diversity, (2) conduct research at the species and population levels impacted by the threats, (3) conduct research at the community level impacted by the threats, and (4) understand the relationship between conservation and sustainable development (Primack, 2000). Underlying all four of these topic areas is the recognition that we wish to conserve ecosystem integrity by preserving life processes as much as conserving biodiversity (Western, 1992).

B. Conservation Biology and Marine Studies

While the principles of conservation biology are routinely applied in terrestrial science and management programs, marine and coastal studies are as much as two decades behind in the application of this discipline to solve the crisis of habitat degradation and biodiversity loss (Murphy and Duffus, 1996). This inequality is clearly obvious when comparing the very small number and size of marine protected areas (MPAs) relative to the numerous reserves, parks and wilderness designations established in terrestrial biomes (Lindholm and Barr, 2001). In the United States the first Federal mandated National Marine Sanctuary was not established until 1975, 100 years after designating the first terrestrial national park. Likewise, among the 123 coastal special protected areas from the Mediterranean, only 45 actually affect the marine environment (CAR-ASP, 1997). There has been a determined worldwide effort toward conserving and protecting charismatic marine vertebrates such as sea turtles and mammals, while habitat conservation has received much less attention. This discrepancy continues despite knowledge that some of the most endangered marine fauna on earth, including sirenians (Aragones and Marsh, 2000; Lefebvre et al., 2000), green sea turtles (Bjorndal 1980), and many fisheries depend on marine habitats such as seagrass meadows for food and nurseries (Heck et al., 1997). A large disparity also exists in

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Abbreviations: EFH - essential fish habitat; FMP - fisheries management plan; GBR - Great Barrier Reef; GBRMP - Great Barrier Reef Marine Park; GBRMPA - Great Barrier Reef Marine Park Authority; IUNC; MPA - marine protected area; NGO - non-governmental organization; UNEP - United Nations Environmental Programme emphasis between terrestrial and marine protection, indicating that an interdisciplinary and comprehensive approach to the conservation of marine biodiversity associated with the biomes like seagrasses is a high priority (Lavery, 2000). In this chapter, we examine the current state of seagrass science within the viewpoint of conservation biology. We discuss areas where seagrass science has been influenced by a conservation biology approach, identify priority research topics for conservation science, give examples where science and conservation biology are being applied in the seagrass biome, and recommend a course of action based on the principles of conservation biology to reverse the global trend of local extinction, fragmentation, and general degradation of the seagrass biome.

C. Seagrass Biodiversity

The sea and the coastal margins, are some the most biodiverse regions on earth (Irish and Norse, 1996). Seagrasses are unique because out of the estimated two to three hundred thousand species of flowering plants they are the only angiosperms that have adapted to life in a submarine environment (Arber, 1920; den Hartog, 1970; Hemminga and Duarte, 2000; den Hartog and Kuo, Chapter 1). With only 12 genera and 50–60 described species, seagrasses themselves are not taxonomically diverse compared to other benthic marine primary producers such as seaweeds and microalgae (Fig. 2; den Hartog, 1970; Green and Short, 2003). Yet, seagrass beds can be long-lived and some are reportedly a 1,000 years old (Reusch et al., 1999). Despite their own limited taxonomic diversity, seagrasses are the only rooted organisms in the near shore region and are the foundation for thousands of other taxa including vertebrate and invertebrate species that use the biome for shelter, foraging sites, spawning habitat, and nurseries (Kikuchi and Peres, 1977; Orth et al., 1984). Protecting the few seagrasses species that exist is essential to the biome and will safeguard species richness, biodiversity, ecosystem structure, and many ecological processes. A loss of just one species of seagrass could cascade throughout an entire coastal ecosystem with long-lasting effects (Preen et al., 1995; Duarte, 2000; Hemminga and Duarte, 2000).

The biodiversity supported by the seagrass ecosystem can be appreciated by examining representative biomes from temperate and tropical regions (Duarte, 2000; Hemminga and Duarte, 2000). In almost every comparison between submerged areas covered by seagrasses and those that are not, species richness, abundance, and diversity of the associated communities are greater within seagrass beds (Howard et al., 1989; Sheridan, 1997). Many of the organisms associated with the seagrass biome drive important ecological processes that take place in coastal systems. For example, invertebrates within seagrass beds transfer energy to higher trophic levels by transforming primary into secondary production (Klumpp et al., 1989; Valentine and Duffy, Chapter 20). The loss of seagrasses alters the flow of organic matter, nutrient cycles, and food webs throughout coastal ecosystems where seagrasses occur and in adjacent ecosystems where seagrasses export organic matter (Kenworthy, 1981; Bach et al., 1986; Preen et al., 1995; also refer to Chapters 7, 8, 21, 24 and 26). The loss of these important ecological processes eventually leads to economic disasters including the collapse of fisheries, degradation of water quality and the decline of other living resources (De Jonge and De Jonge, 1992).

The Great Barrier Reef (GBR) region of northeastern Australia is one of the most conspicuous examples of seagrass biodiversity and bio-connectivity known. Frequently referred to as the rainforest of the sea, the GBR ecosystem has 15 species of seagrass including nearly 6,000 km^2 in water less than 15 m deep and as much as 40,000 km^2 of seagrass in deeper water (Lee Long et al., 2000). The seagrass and invertebrate communities of the GBR provide water column and benthic structure for thousands of other invertebrate taxa, 1,500 species of fish, 4,000 species of molluscs, 5 species of turtles, 250 species of birds, and one of the four remaining large herbivorous marine mammals, the threatened dugong. Throughout the GBR seagrasses make frequent contact with coral reefs and other live bottom communities and the interconnectivity between the reef and seagrass communities is ecologically very important. The GBR region serves as a good example of the great potential for structural and functional biodiversity in the seagrass biome that needs to be conserved.

D. Diversity of Seagrass Ecosystem Services

The seagrass biome provides a diversity of ecosystem services sometimes difficult to quantify

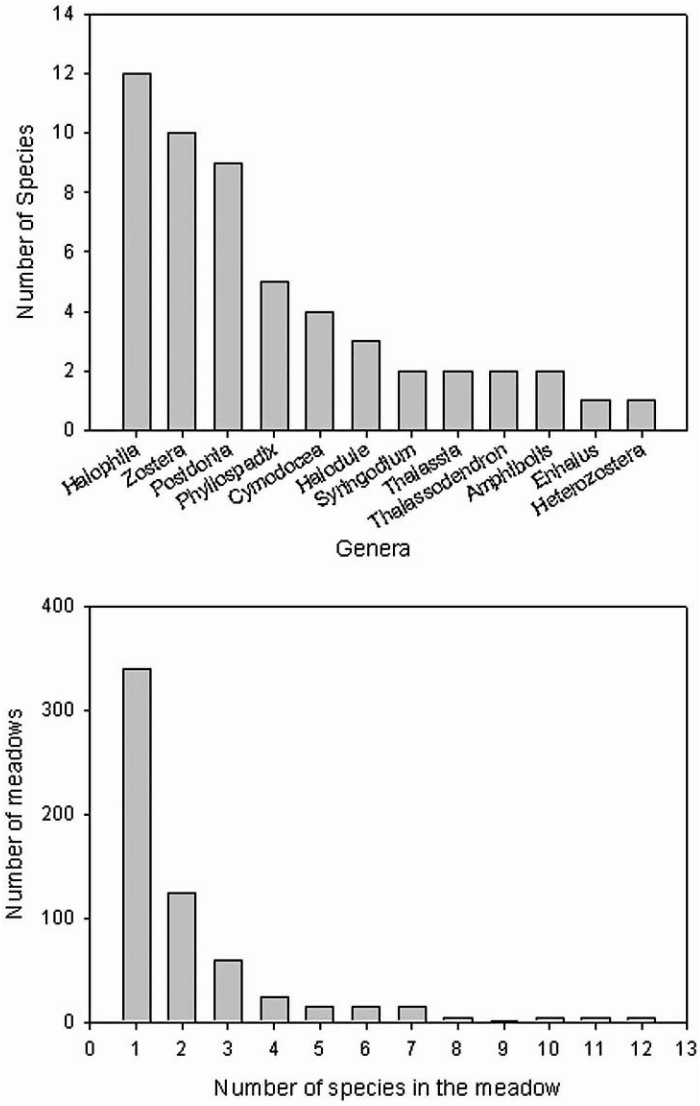


Fig. 2. Number of seagrass species in each seagrass genus (top panel) and frequency of meadows versus the number of species per meadow (bottom panel). Bottom panel from Duarte (2000), with permission.

(Costanza et al., 1997; Duarte, 2000; Fonseca et al., 2000a, 2002a). The rich diversity of resident and migratory fish and invertebrates contributes to the selection of this biome as a favored gathering and hunting site for coastal people (Suttles, 1951; Fortes, 1990; Green and Short, 2003). Humans and coastal systems also derive benefits from the interaction between seagrasses and sediments. Seagrasses filter the water column of sediments and organic matter (Kenworthy et al., 1982), stabilize the substrate with their roots and rhizomes (Fonseca and Fisher, 1986), recycle large amounts of nutrients (Klumpp et al., 1989), export organic matter to adjacent systems (Bach et al., 1986), and mitigate coastal eutrophication (Dennison et al., 1993). Seagrass canopies baffle wave and tidal energy protecting subtidal sediments and shorelines from erosion to the extent of forming seagrass 'banks' that can alter local and regional hydrography and directly affect biota (Fonseca and Fisher, 1986; Fonseca and Bell, 1998). The accumulation of dead leaves on the shore enhances the formation of dunes that can prevent beach erosion (Gambi et al., 1989; Madsen et al., 2001).

The most difficult ecosystem services to quantify are the intrinsic values of natural systems, such as the beauty of a lush seagrass meadow and the functions that do not have obvious immediate value to society. Some services are deeply rooted in native cultures where ethnobotanists have identified seagrass cultural values ranging from food to medicine (Wyllie-Echeverria et al., 2000). Particular cultures have integrated seagrasses into their traditional hunting and ceremonial life. These historical and cultural attributes provide an alternative way of assigning conservation value to seagrass systems previously not emphasized in legal and judicial processes. Simply stated, ‘people tend to conserve what they cherish and use (Wyllie-Echeverria et al., 2000).

E. Economic Value of the Seagrass Biome

The economic values of the seagrass biome are difficult to calculate within a traditional market analysis; however, Virnstein and Morris (1996) and Costanza et al. (1997) provided what they described as minimum estimates for seagrass and algal dominated systems. Based on published reports, Costanza et al. (1997) assessed the annual value to be U.S. \$19,004 ha^{-1} year^{-1}, with primary value derived from nutrient cycling and the supply of raw materials. Because this estimate does not include values associated with fishery stocks (spawning, rearing, and refuge habitat), the sustainability of marine mammals, waterfowl, and turtles, beach protection, or value associated with intrinsic worth, the figure is an underestimate of actual worth. Based on fishery value alone, Virnstein and Morris (1996) estimated that the 80,000 acres (32,375 hectares) of seagrass in the Indian River Lagoon, Florida were worth approximately one billion dollars (U.S. currency) per year.

When seagrasses are damaged, restoration of the seagrass biome is expensive and uncertain, and many of the lost ecological services are not adequately restored (Fonseca et al., 1998; Fonseca et al., 2000a, 2002a). Replanting techniques have been used to a limited extent for a small number of species, primarily *Zostera marina, Thalassia testudinum, Halodule wrightii,* and *Posidonia oceanica* (Orth et al., 1994; Molenaar and Meinesz, 1995; Balestri et al., 1998; Fonseca et al., 1998), but documentation of success is rare. Recent estimates for the cost for restoring tropical seagrasses in the United States range from approximately U.S. \$100,000 per acre (0.4 hectares) for moderate disturbances to as much as a million dollars per acre in the worst cases where sediments are physically disturbed. In most instances, the cost of restoration and the assessments of success are based on very small-scale projects. Probably, no one has correctly estimated the cost of restoring an entire seagrass ecosystem or biome and even many of the smaller scale attempts at restoration have failed (Fonseca et al., 1998). The temptation to use replanting to justify new seagrass destruction underscores the urgency that such mitigation activities must be closely monitored, controlled and prevented unless they are deemed socially acceptable (Fonseca et al., 1998; Fonseca et al., 2002a; Boudouresque, 2000). Successful seagrass restoration should be implemented with clearly defined objectives that measure success in regional and global terms (Campbell, 2000; den Hartog, 2000; Orth, 2000). For example, a decision framework proposed for the restoration of *Posidonia oceanica* in the Mediterranean region recommends only activities that are initiated and completed by the use of a ‘code of good conduct’ system emphasizing the point that ‘replanting cannot be done as compensation for deliberate seagrass destruction.’ The intrinsic value of seagrasses, coupled with high restoration costs and uncertainty of success, suggest that we prioritize the benefit of conservation programs that minimize injuries to the seagrass biome and make every attempt to avoid the expensive and uncertain repair of damaged ecosystems.

F. Cultural Value of the Seagrass Biome

Crustaceans, bivalves, egg masses, and fish associated with the seagrass biome have sustained and continue to sustain coastal people in temperate and tropical environments (Suttles, 1951; Felger and Moser, 1985; Fortes, 1990; Kuhnlein and Turner, 1991; Wyllie-Echeverria et al., 2003; Bandeira and Gell, 2003). Valued hunting and gathering sites are often protected by cultural traditions nested within mythological and social beliefs (e.g. Kurien, 1998; Berkes et al., 2000). Food collected from these sites supplements resources purchased in the market-based economy (e.g. Turner et al., 2000). Seagrass leaves from several species (*Z. marina; Thalassodendron ciliatum*; *Enhalus acoroides*; *P. oceanica*; *Phyllospadix iwatensis; P. torreyi*) are gathered from the wrack line or cut above the surface of the sediment, dried, and used for thatch, animal bedding, mattress and pillow stuffing, and cordage (Felger and Moser, 1985; Wyllie-Echeverria and Cox, 1999; Aioi and Nakaoka, 2003; Bandeira and Gell, 2003; Ochieng and Erftemeijer, 2003; Procaccini

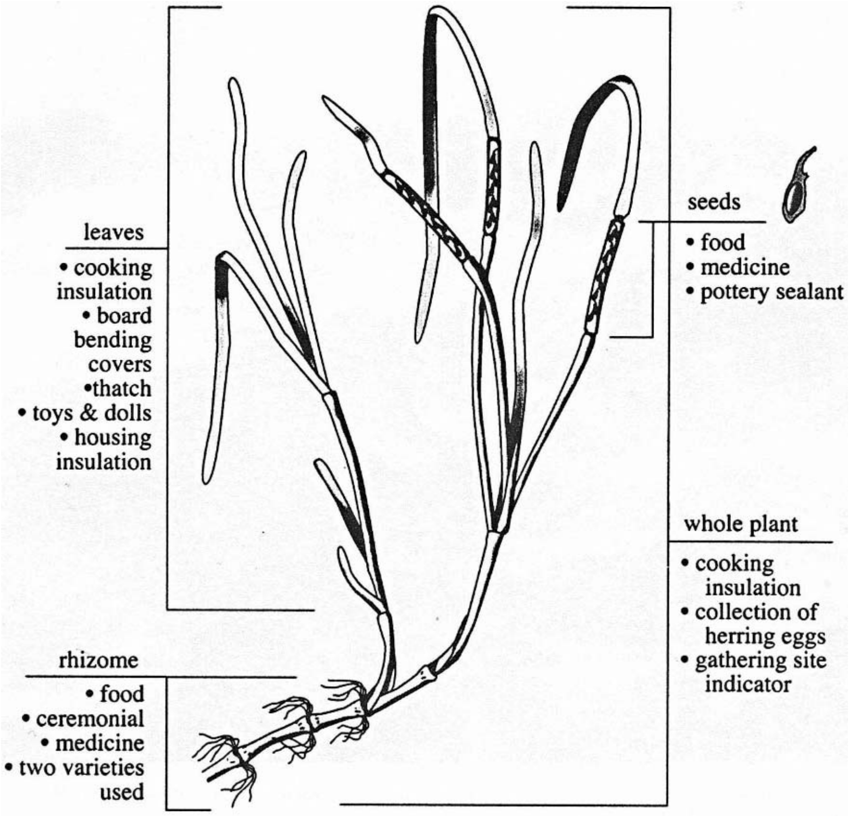


Fig. 3. List of natural products derived from *Zostera marina* (from Wyllie-Echeverria et al., 2000).

et al., 2003; Coles et al., 2003). The seeds (raw) and rhizomes (ground into flour) of *E. acoroides* are also eaten (Bandeira and Gell, 2003; Ochieng and Erftemeijer, 2003) and *Halophila ovata* leaves are a principal ingredient in a paste used to treat various skin ailments (Parthasathy et al., 1991).

Studies in the North Atlantic (Wyllie-Echeverria et al., 2000), the Gulf of California (Felger and Moser, 1985), and British Columbia in Canada (Kuhnlein and Turner, 1991) reveal the importance of the seagrass *Z. marina* to subsistence cultures for many generations. These cultures derive many and varied natural products from this plant (Fig. 3) and their recognized historical value contributes to the protection of sites of former gathering activity (e.g. Wyllie-Echeverria et al., 2000; Wyllie-Echeverria and Ackerman, 2003). Ethical positions regarding the value of resource extraction are common among traditional and indigenous cultures, often leading to the protection of habitats that support valuable resources (Williams and Hunn, 1982; Escamilla et al., 2000). In these societies, frequently against pressure from development interests, strong effort is advanced to prevent habitat alteration (Cox and Elmqvist, 1991; Cox and Elmqvist, 1993).

Evidence suggests that particular seagrass species had value even before the development of market-based economies. In the Channel Islands, off the coast of California in the United States (34 N; 120 W), the Coastal Chumash began to fashion cordage, thatch and footwear from the leaves of *Phyllospadix torreyi* more than 8,000 B.P (Fig. 4; Salls, 1988; Connolly et al., 1995). For these coastal people, the thin, silicate strengthened leaves of this plant provided raw material needed to weave fishing line and thatch shelters for thousands of years, suggesting that collecting sites and plant populations were valued. While it is more difficult to demonstrate the intrinsic value of these wild plants in agricultural and industrial societies, there is tangible evidence that the splendor and function of seagrass species enhances both poetry and art within these cultures (Fig. 5) (Darwin, 1791; Standing et al., 1975; Whitt, 1988).

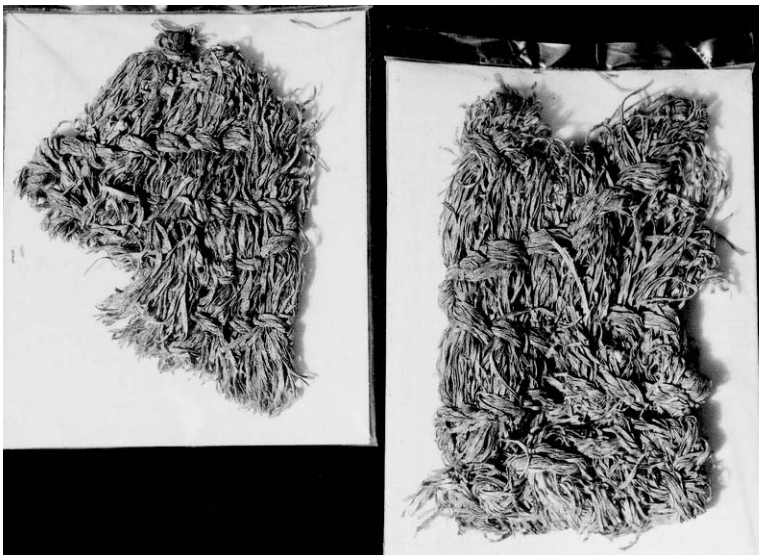
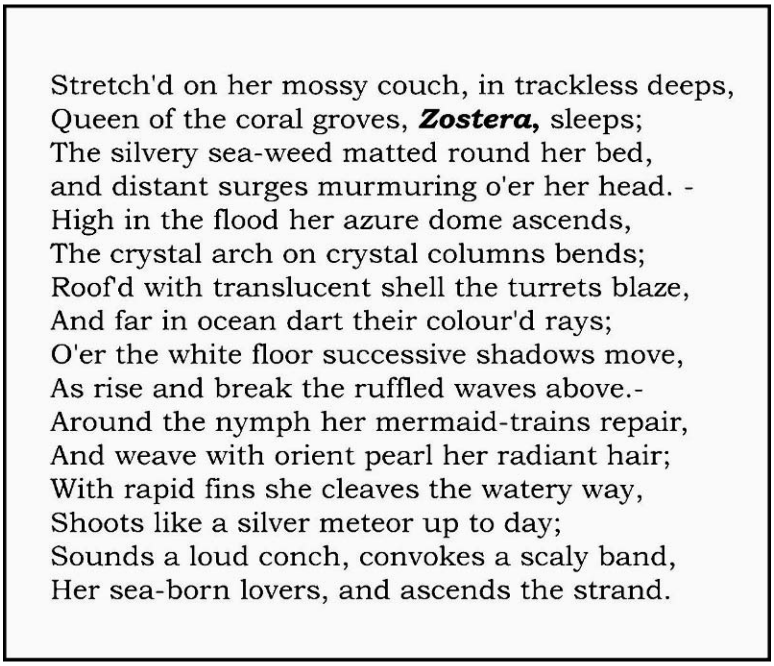


Fig. 4. This ancient sandal was woven from the leaves of *Phyllospadix torreyi* by the Coastal Chumash approximately 8,000 B.P. (Courtesy of the Santa Barbara Museum of Natural History).

G. The Need for a Conservation Biology Program Directed at the Seagrasses Biome

Norse (1993) argues that there are five serious threats to marine biodiversity: (1) overexploitation of natural resources, (2) physical alteration of habitat and substrate, (3) nutrient and sediment pollution, (4) introduction of alien species, and (5) global climate change. These five threats often co-occur and the combination of natural disturbance and



Stretch'd on her mossy couch, in trackless deeps,
Queen of the coral groves, ***Zostera,*** sleeps;
The silvery sea-weed matted round her bed,
and distant surges murmuring o'er her head. -
High in the flood her azure dome ascends,
The crystal arch on crystal columns bends;
Roof'd with translucent shell the turrets blaze,
And far in ocean dart their colour'd rays;
O'er the white floor successive shadows move,
As rise and break the ruffled waves above.-
Around the nymph her mermaid-trains repair,
And weave with orient pearl her radiant hair;
With rapid fins she cleaves the watery way,
Shoots like a silver meteor up to day;
Sounds a loud conch, convokes a scaly band,
Her sea-born lovers, and ascends the strand.

Fig. 5. This stanza is from a larger poem entitled 'The Loves of the Plants: A Poem' and was written by Erasmus Darwin (1791) – see, also "Foreword" to this volume.

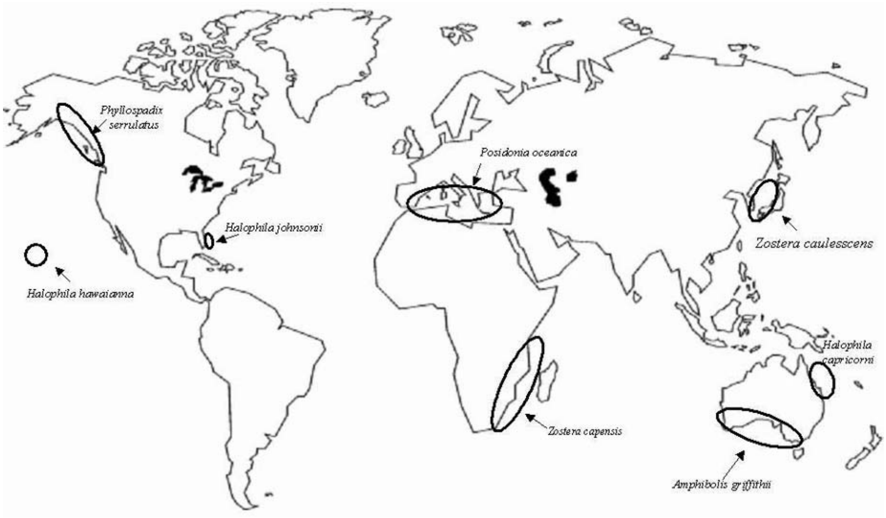


Fig. 6. Examples of endemism and restricted ranges within the seagrass flora are illustrated in different regions. Species are *Phyllospadix serrulatus, Halophila johnsonii, Halophila hawaiiana, Halodule emarginata, Halophila capricorni, Zostera capensis, Amphibolis griffithii, Cymodocea angustata, Posidonia oceanica.*

anthropogenic stressors exacerbate the effects of any individual threat. Although five seagrass species—*E. acoroides, H. johnsonii, H. decpiens, Z. asiatica, and Z. caulescens*—have been formally recognized by national governments as vulnerable or threatened, (vulnerable stage according to the Red Data Book of Japan and Endangered Species Act (ESA), United States National Marine Fisheries Service, September 14, 1998, FR 49035), threats to biological diversity in seagrass systems are more widespread than realized. Recent literature that summarized natural and anthropogenic impacts on seagrasses suggests the efficacy of establishing a conservation biology approach to protect the seagrass biome (Short and Wyllie-Echeverria, 1996; Duarte, 2002). Here, we address issues of resource protection, management, and discuss examples of research priorities that we think are the most critical areas of science needed to support a seagrass conservation biology perspective in the future.

In general, seagrasses grow throughout the world on unconsolidated sediments in nearshore tropical and temperate waters that are influenced by the coastal marine environment (den Hartog, 1970; Phillips and Menez, 1988; Green and Short, 2003) (*Thalassodendron* and *Phyllospadix* spp being the exception). In the coastal zone the interface between land and sea and air and water provide a complex recipe of environmental conditions where some of the most intensive and extensive human occupation, commercial development, industrialization, and resource extraction occur. The level and complexity of natural and human stressors that affect the seagrass biome and threaten its' biodiversity are well recorded (Short and Wyllie-Echeverria, 1996; Duarte, 2002). Important as well is the fact that the seagrass flora is not nearly as taxonomically diverse as terrestrial and freshwater angiosperms (Philbrick and Les, 1996; Hemminga and Duarte, 2000) (Fig. 2). The relatively low biodiversity of seagrass taxa is also manifested by several endemic species with very narrow geographic ranges (Fig. 6).

The low diversity of seagrass species has important ecological implications. In many locations seagrass beds are monospecific (Fig. 2, bottom panel) (Hemminga and Duarte, 2000), so the loss of just one seagrass species can result in the loss of the entire structural attribute of a coastal system with the formation of large gaps in seagrass coverage that diminish the spatial continuity of ecological services (Fonseca et al., 2002a). In tropical beds, even where several species occur in the same region, individual species are heterogeneously distributed across the landscape. Contiguous beds will often be a mosaic of monospecific patches interspersed with patches of co-occurring species typical of clonal growth (de Kroon and van Groenendael, 1997). Because of this pattern of species' distributions, beds that appear to be contiguous are vulnerable to species-specific declines.

H. Ecological Implications of Seagrass Biodiversity

There are two global hotspots of high seagrass species diversity—the Indo-Pacific and the Red Sea—where as many as 10–15 species can co-occur. Even in these two regions there is considerable spatial partitioning among species with depth zonation and gaps between individual species within contiguous meadows. In these beds, when one species declines the time scale over which it recovers or is replaced by another seagrass species can be quite long (Birch and Birch, 1984; Williams, 1990; Preen et al., 1995; Kenworthy et al., 2002; Peterson et al., 2002). In some examples of disturbance, no recovery has been observed (Whitfield et al., 2002), or species may be replaced by macroalgae (Williams, 1990; Hauxwell et al., 2001). Low rates of recovery are due to the fact that many species rely on vegetative reproduction and clonal growth (Duarte et al. Chapter 11). Spreading rates by rhizome extension and the re-occupation of space from ramet expansion is typically <1–3 m year^{-1} (Marbà and Duarte, 1998; Fonseca et al., 2004). Some species re-occupy gaps quite rapidly from a sediment seed bank, clonal growth, and vegetative fragment dispersal (Birch and Birch, 1984; Philbrick and Les, 1996; Kenworthy, 2000; Inglis, 2000a,b; Peterson et al., 2002; Hammerstrom and Kenworthy, 2003; Walker et al., Chapter 23), but this may actually lead to a temporary shift in species dominance (Fourqurean et al., 1995) or the absence of species during less than optimal growing conditions (Kenworthy, 2000). Recent studies in the multispecies meadows of the Philippines, where as many as seven seagrasses co-occur, showed that the presence of one species controlled the distribution of other species in the same area (Terrados et al., 1998; Duarte, 2000). When one of the dominant species was experimentally removed from this community, four others declined, leading to the loss of biodiversity and formation of gaps within the meadow.

I. Conservation Biology and Large-Scale Declines of Seagrasses

Large-scale declines in seagrass populations have been documented from at least 40 locations worldwide as a result of both natural processes and human activities (Orth and Moore, 1983; Preen et al., 1995: Short and Wyllie-Echeverria, 1996; Hemminga and Duarte, 2000; Duarte, 2002; Walker et al., Chapter 23). The most famous example of natural decline was the ‘wasting disease’ of mono-specific *Z. marina* populations on both the American and European coastlines of the north Atlantic during the 1930s (Rasmussen, 1977; Moore and Short, Chapter 16). The precise cause was likely due to a pathogen and the magnitude of loss associated with this natural catastrophe is still debated today (Muehlstein, 1992). In some areas recovery was either slow or nonexistent (Cottam and Munro, 1954; Thayer et al., 1984). Slow recovery of *Z. marina* populations resulted in large changes to the physical and chemical conditions of the sediments and colonization by other benthic vegetation, mainly macroalgae (Rasmussen, 1977).

An event such as the wasting disease could have even more severe and longer-lasting consequences today than those experienced in the mid-1900s. Recovery of *Z. marina* populations coincided with the early stages of the large-scale modern day industrialization and human occupation of coastal environments in the North Atlantic. If the demographic trends proceed as forecasted, human population in the coastal zone will continue to grow, causing more extensive and intensive anthropogenic stress than occurred when the wasting disease prevailed (Duarte et al., 2002; Green and Short, 2003). These activities include inappropriate fishing methods and overfishing, eutrophication, water diversion, shoreline armoring and destabilization, freshwater diversion, agriculture, industrialization, and the anticipated consequences of global climate change. The combined impact of these stressors and disease has the potential for eliminating *Z. marina* from many locations.

It is clear that while humans lack control over particular types of natural disturbances that can affect seagrasses such as disease, orogenic uplift, and volcanic eruption, science and technology exist to arrest and contain the impacts of industrialization and human occupation of the coastal zone. Conservation biology makes the direct connection between human activities, habitat loss, and local extinctions (Primack, 2000). Although this approach has been extended to aquatic ecosystems, only recently has a conservation biology framework been focused directly on the seagrass biome (Special Issue of Pacific Conservation Biology Volume 5(4) 2000; Coles and Fortes 2001; Green and Short, 2003). This chapter emphasizes the need for a conservation biology perspective in seagrass science and the initiation of research projects guided by the principles of this discipline.

II. The State of Seagrass Science Relative to Conservation Biology

While biogeographic and descriptive studies were done in the early years of seagrass science (Setchell, 1920), publication of 'The Seagrasses of the World' (den Hartog, 1970) initiated the modern era of seagrass ecology. Soon after, the first International Seagrass Workshop was held in Leiden, The Netherlands in October 1973. At this meeting an international body of scientists, representing 11 nations, recommended a series of research goals designed to promote an interdisciplinary program focused on the study of the seagrass biome (McRoy, 1973). Supported by the U.S. National Science Foundation, International Decade of Ocean Exploration (IDOE), the workshop was stimulated by the long-held view of the important ecological role of seagrasses based on fisheries research in Denmark late in the 1800s (Peterson, 1915), and led to coordinated research projects in the U.S., Central America, Europe, Asia, and Australia. The IDOE Seagrass Ecosystem Study educated many graduate students, supported national and international research projects, and resulted in several textbooks (e.g. McRoy and Helfferich, 1977; Phillips and McRoy, 1980), a growing list of workshops (Boudouresque et al., 1984, 1989) and publications that fueled continuing expansion of seagrass related studies (Larkum et al., 1989; Duarte 1999; Hemminga and Duarte, 2000; Short and Coles, 2001; Green and Short, 2003).

Seagrass scientists began meeting in regular organized forums entitled International Seagrass Biology Workshops starting in 1993. Many of the developing nations represented at these meetings had no formal seagrass conservation programs and were prime candidates for initiating a global effort. The first workshop was held in Kominato Marine Laboratory (University of Tokyo), Japan in 1993 with scientists from several countries attending (Aioi, 1993). The meetings that followed (Rottnest Island, Western Australia; Manila, The Philippines; Corsica, France, Ensenada, Mexico and Townesville, Australia) included proceedings describing the current state of the science (Kuo et al., 1996; Duarte and Fortes, 1999; Pergent et al., 2000; Ibarra-Obando, 2003). The rapid spread of scientific interest in seagrass systems resulted in the usual diversification and specialization within an expanding research field. Between 1989 and 1997 the annual seagrass publication rate doubled every four years, yet approximately 90% of the publications were concentrated in only four marine journals with few in general ecology or conservation biology (Duarte, 1999). Even though studies continued to be dominated by descriptive research, the interest in seagrasses expanded into many disciplines, including synthesis and modeling to the benefit of conservation biology.

One of the first efforts to formally incorporate seagrass ecology into a conservation biology context and promote a global cooperative framework for protecting seagrass biomes took place in Sydney, Australia at the Society for Conservation Biology Symposium in 1998 (Special Issue of Pacific Conservation Biology, 2000: 5(4)). This symposium coincided with the heightening of worldwide awareness for marine biodiversity and included papers covering several aspects of seagrass conservation, from genetics and population biology to threatened marine herbivores and cultural values.

With these publications and the heightened awareness of the value of seagrasses, scientists, and the public are recognizing the difficulty in making decisions and implementing policies for coastal management with generic conservation value (Coles and Fortes, 2001). However, it is true sadly that the seagrass biome continues to suffer from the fact that mismanagement occurs in many countries because no group individual or organization has vested interest in the sustainability of the biome, a phenomenon generally identified by Hardin (1968) as the 'Tragedy of the Commons'. Seagrasses grow on submerged lands that are often held in common trust by a community with limited private ownership and may even cross state, territorial, and international jurisdictions. The effects of policies and activities implemented outside local jurisdictions but connected by the fluid medium of rivers, estuaries, and coastal currents can lead to fragmentation or local extinction of the seagrass biome. Many secondary consumers that migrate between connected bodies of water rely on seagrass and are especially vulnerable to the possible lack of uniform control over practices within the separate locations. Unfortunately, decisions in one jurisdiction may not influence policy in adjacent jurisdictions, but it is critical to understand the importance of connectivity among and between widely dispersed elements of the seagrass biome (e.g. Roberts, 1997; Jameson et al., 2002).

One of the many fundamental roles science must take in the conservation of seagrasses is to identify the processes linking coastal systems and educate resource managers and the public on this connectivity before effective geographical boundaries of conservation actions can be defined (sensu Jameson et al., 2002). In this activity the value of different scientific disciplines working together in conservation biology must be recognised (e.g. landscape ecologists, physical oceanographers, and biogeographers). With widespread acknowledgement of a ‘crisis of degradation’ in marine biomes around the globe, especially the deterioration of fisheries and their habitats, the stage is set to focus marine scientists and seagrass ecologists on the principles of conservation biology beyond the charismatic megafauna, in order to develop a comprehensive program of sustainable resource management (sensu Duarte, 1999).

III. Seagrasses Conservation Biology: An Approach for the Future

A. What Managers Need

Scientists and managers are faced with both short- and long-term resource management problems at a variety of spatial scales that require an adaptive approach in identifying research priorities. A fundamental challenge for science is to develop predictive capabilities that managers can use at different temporal and spatial scales (Fonseca, 1996; Duarte, 1999; Virnstein, 2000; Duarte, 2002; Fonseca et al., 2004). Many problems need to be resolved immediately, without benefit of input from lengthy, carefully designed, and replicated experiments to determine the best management practices for conservation purposes. Quite often, managers must make decisions in a situation of urgency with a paucity of data. Consequently, the synthesis of existing information (e.g. Duarte, 2002) and ‘real time’ applied science is extremely relevant to adaptive management (e.g. Kenworthy et al., 2002; Orth et al., 2002; Whitfield et al., 2002).

Scientists must provide managers with the information and tools necessary to meet the conservation needs articulated by the public and resource managers. These needs are currently addressed by several different types of management actions, including but not restricted to: (1) statutory authority (prescriptive approaches), (2) general consensus (non-prescriptive approaches), (3) a response to identification of lost or damaged resources (restoration), or (4) application of socio-cultural principles. Within this framework of defined actions we can identify the main elements of seagrass conservation biology as; (a) basic hypothesis testing, descriptive science and quantitative synthesis; (b) applied science that develops the tools for conservation of biodiversity using the results of (a) and adapting recommendations to changing needs; (c) scientific support for the development and implementation of tools that managers and the public use to protect seagrass biomes; and (d) interpretation and application of social and cultural values for the benefit of conservation. Element (a) includes basic research in traditional fields such as biology, chemistry, physics, and ecology (Brussard, 1991), but seagrass science has been dominated largely by descriptive work and now should focus more on hypothesis testing, synthesis and prediction to guide conservation decisions (Duarte, 1999). In elements (b) and (c) scientists interact with a broad spectrum of resource managers and stakeholders to formulate tools for conservation. These two elements depend heavily on feedback among science, management and the public, and frequently require scientists to make uncertain predictions and recommendations with limited data and shifting management goals. One of the most important aspects of this process is the quality of the dialogue between scientists and all stakeholders. The fourth element attempts to link existing conservation policies to historical cultural values for the benefit of conservation.

In all four elements the rigor of the scientific method must be maintained to assure that information is valid and defensible in management and litigation forums. In addition, scientific results must be transferred to managers and to the public in a format appropriate for effective translation into conservation tools. Scientific ideas and judgments resulting in the ideas must be comprehensible to managers and user groups so that the full scope of management consequences can be understood, discussed and debated. Finally, scientific solutions must be legally defensible, because the risk that particular decisions will be challenged by those seeking alternative forms of resource management is high (e.g. Fonseca et al., 2000a).

B. Priority Research Topics for Seagrass Conservation Science

1. Habitat Fragmentation and Disturbance Dynamics

Seagrass biomes often occur as an assembly of small, fragmented populations in a patchy distribution but may also be distributed in distinct zonation patterns across the seascape (Fonseca et al., 2000b; Fonseca et al. 2002b; Bell et al., Chapter 26). The existence of patchy seagrass biomes occurs naturally in many ecosystems and may be the equilibrium condition for a particular set of environmental conditions (Marbà and Duarte, 1995; Fonseca and Bell, 1998; Fonseca et al., 2000b; Duarte et al., Chapter 11). While much has been learned about the physical and biological formation of these fragmented populations (den Hartog, 1971; Patriquin, 1975; Fonseca and Bell, 1998; Rose et al., 1999), we know little about the species level mechanisms that maintain patch configuration (Fonseca and Bell, 1998; Marbà and Duarte, 1998; Fonseca et al. 2000b). However, transformation of seagrass beds from continuous cover to a fragmented landscape may increase the vulnerability of these systems to further biophysical degradation. Practices related to aquaculture, commercial fishing, motor vessels, docks, and channel dredging endanger the physical integrity and structure of seagrass meadows leading to fragmentation and altering species abundance and richness (Peterson et al., 1987; Dimech et al., 2000; Ruiz et al., 2001; Kenworthy et al., 2002; Orth et al., 2002; Uhrin and Holmquist, 2003). Practices associated with access to the coastal zone, navigation and the economic incentives related to the harvest of resources in the short-term, may impair the stability of the biome and compromise sustainability over time.

The transformation of the seagrass biome from continuous cover to a patchy, fragmented landscape is not limited to harvest practices but extends to a wide variety of recreational and industrial use of our waterways and the desire for people to live near coastal resources. Aerial photographs reveal scars left by propeller rotation in the soft sediment matrix that supports seagrass growth (Sargent et al., 1995; Whitfield et al., 2002; Kenworthy et al., 2002). Circular patterns of unvegetated areas within continuous seagrass cover are created by the swing of anchor chains, mooring lines, shellfish harvesting, and trawling practices (Walker et al., 1989; Pasqualini et al., 1999; Orth et al., 2002). Over-water structures, providing easy access for recreational boats and commercial ferries, shade the bottom and eliminate seagrass cover (Thom et al., 1998; Burdick and Short, 1999; Shafer, 1999). These activities are fragmenting the landscape and cumulatively impacting the seagrass biome. Examples from landscape-level ecological studies of seagrasses illustrate the relevance of the contiguity of seagrass beds and patch dynamics to bed structure (den Hartog, 1971; Marbà and Duarte, 1995; Bell et al., Chapter 26), seagrass distribution (Fonseca et al., 2002b), survival (Fonseca et al., 2000b), response to natural energy regimes (Patriquin, 1975; Marbà and Duarte, 1995; Fonseca and Bell, 1998; Fonseca et al., 2000b), and community composition (Zieman, 1972; Uhrin and Holmquist, 2003).

The fragmentation and degradation of the seagrass biome become especially perilous in developing nations, as coastal states attempt to increase revenue through activities that elevate stress levels in seagrass ecosystems (e.g. Wu et al., 1998; Cloern, 2001). A conservation biology perspective that recognizes the interdependence of ecosystem function and societal need can help prevent fragmentation and degradation of seagrass biomes in developing nations.

Fragmentation can threaten biodiversity and the structure and function of the seagrass biome. With so few seagrass species locally and globally and numerous examples of endemism, the loss of a single species is potentially catastrophic to hundreds or thousands of other organisms, as well as the degradation of many important ecosystem processes. Because it is difficult to separate the signal (human disturbance vectors) from the noise (natural variability of disturbance), the role of disturbance and the response of seagrass species to a particular disturbance should be a major focus of long- and short-term research programs. Disturbance ecology should not be limited to just mapping and cataloging changes associated with natural and human events, but should also include detailed ecological studies identifying the direction of change and the mechanistic processes involved in controlling response and recovery dynamics in order to predict their ecological consequences (Fourqurean et al., 1995; Whitfield et al., 2002; Kenworthy et al., 2002; Peterson et al., 2002).

2. Multiple Stressors

A comprehensive research agenda is needed to predict the response of the seagrass biome to multiple stressors, especially when considering the consequences of global climate change, resource extraction by fisheries, and the growing human population in the coastal zone (Short and Neckles, 1999; Section IV, Ralph et al., Chapter 24). The selection and application of appropriate management regimes depends on the ability to distinguish natural from human stressors (sensu Jameson et al., 2002). For example, there is strong evidence suggesting that increases in nutrient loading and siltation, two stressors often co-occurring in disturbed systems, can lead to long-term shifts in taxonomic composition of seagrass communities by placing extraordinary physiological demands on the biota (Borum, 1985; Tomasko and Lapointe, 1991; Nixon, 1995; Fourqurean et al., 1995; Short and Burdick, 1996; Terrados et al., 1998; see also Walker et al., Chapter 23 and Ralph et al., Chapter 24). Many seagrasses have complex life histories which are affected by different stressors over their lifetime and the distribution, abundance and species composition of the biome results from many different factors operating at varying spatial and temporal scales, and seldom isolated from one another.

In the Mediterranean, the input of nutrients resulting from aquaculture activities was responsible of significant declines of a *P. oceanica* meadow around fish farming facilities (Pergent et al., 1999; Cancemi et al., 2000; Dimech et al., 2000). Prior to the placement of the fish farm, these meadows were considered 'healthy and productive' but appear to have been negatively affected by a single human stressor, the introduction of aquaculture. Thus, if healthy meadows are so readily affected, it will be important in the future to understand how beds already stressed respond to additional stressors such as aquaculture practices.

Mass mortality of seagrasses over very large areas of an entire subtropical estuary in south Florida, USA (Florida Bay; 25.00 N; 80.45 W) fragmented the seagrass system resulting in a cascade of impacts affecting both the benthic and pelagic communities in a much larger geographical region (Roblee et al., 1991; Fourqurean and Roblee, 1999; Walker et al., Chapter 23). The causes of this mass mortality were hypothesized to result from a combination of factors including water diversion, eutrophication and an unusually advanced community succession in the absence of physical disturbances associated with an abnormally low recurrence of hurricanes in south Florida. This example demonstrated that the magnitude and complexity of these multiple factors must be taken into account in developing a plan for restoration of Florida Bay, because it is located within a dynamic and interconnected system of uplands, wetlands, estuaries, reef tract, and continental shelf (Jameson et al., 2002). The south Florida region is one of the most densely populated coastal zones in North America where human stressors are numerous and widespread. Landscape scale studies integrating biology, physical sciences, and socio-economics will be needed to forecast the future of this seagrass biome under different management and restoration scenarios incorporating multiple stressors (see Bell et al., Chapter 26).

Studies in the vicinity of urbanized estuaries and industrial areas have documented reduced plant fitness from heavy metal contamination associated with industrial development (Lyngby and Brix, 1984; Pergent-Martini, 1998; Ralph and Burchett, 1998; Capiomont et al., 2000; Prange and Dennison, 2000; Ralph et al., Chapter 24), and although metals are probably not biomagnified (Ward, 1989), transfer of metal toxicity to consumers has been suggested (Prange and Dennison, 2000). Seagrass biomes are exposed to a wide range of pollutants that need to be factored into the equation of multiple stressors, especially when the affects cascade up and down food webs or are confounded by the absence of grazer species lost through overfishing. These stressors include nonpoint source pollution, waste treatment, agricultural as well as industrial practices and toxic substances found in fertilizers, pesticides, herbicides, and fungicides.

3. Scale Factors

The conservation and management of seagrasses requires approaches at multiple scales (Fonseca, 1996; Virnstein, 2000). Every attempt to describe the biome by mapping, monitoring or process-oriented studies must consider the effect of scale on the proposed research question. Linkages and connectivity between seagrasses and other species and with adjacent systems should be an integral part of this research, including the construction of models robust enough to forecast change at local, regional, and global scales (Duarte, 2002). The fluid medium surrounding the seagrass biome is seldom bounded by discrete barriers. Organisms and water constituents move between systems, therefore, management actions in one system can have a direct effect on another system, and in many instances these can occur at very large scales (Roberts, 1997; Jameson et al., 2002; Johnson et al., 2003). Attributes associated with conservation biology can be used to organize research programs addressing different scales. Broad scale research programs linking upstream watershed activities with investigations in the estuary, the reef tract, and the coastal shelf are needed to effectively conserve and protect seagrasses. This is an opportunity for landscape ecologists, physical oceanographers, and remote sensing specialists to collaborate with biologists, ecologists, geographers, and social scientists to synthesize information and construct holistic models for seagrass conservation.

4. Invasive Species

Biological invasions threaten the structural integrity and function of natural systems of plants and animals (Carlton and Geller, 1993; Walker and Kendrick, 1998). There are only a few examples of the interactions between non-native and indigenous species involving seagrass ecosystems; however, with the globalization of trade and the predictions for climate change, there are likely to be more issues associated with species invasions in the future. The only known large-scale displacement of seagrasses by an invasive species has been documented in the Mediterranean, where an introduced green alga, *Caulerpa taxifolia*, has had a negative impact on the seagrasses *P. oceanica and C. nodosa* (Meinez et al., 1995; Ceccherilli and Cinelli, 1997; Dumay et al., 2002). Additionally, the extension of a new *Caulerpa* species (*C. racemosa*) in the same region induced similar effects (Dumay et al., 2002; Piazzi and Ceccherilli, 2002). The discovery of *C. taxifolia* in southern California (Williams and Grosholz, 2002) suggests that future interactions involving other seagrass species and nonnative introductions by macroalgae may occur. While the scientific community is still debating the ecological implications of the *Caulerpa* species invasions, introduction of macroalgae into nonnative coastal plant communities may become more common and problematic than previously believed (den Hartog, 1997). *Sargassum muticum* can threaten the patch stability of *Z. marina* if meadows are beginning to fragment (den Hartog, 1997), but no wide spread outbreaks of *S. muticum* have yet been reported.

In the Great Bay Estuary of New Hampshire in the United States, the European green crab (*Carcinus maenas*) affects the survival of transplanted *Z. marina* by shredding the leaves and destroying apical meristems (Davis et al., 1998). Bioturbation is not uncommon in seagrass meadows and sometimes serves as an important mechanism for recycling nutrients, as a disturbance vector, or may act as a key natural stressor (Orth, 1975; Suchanek, 1983); however, the presence of the non-native green crabs threatens the restoration potential of *Z. marina* meadows in the northeastern United States. Without some form of caging to protect the seagrasses or some modification of the shredding behavior, green crabs effectively destroyed recently transplanted eelgrass.

The introduction of non-native seagrasses has been documented in at least two instances. *Zostera japonica* was first reported in the Pacific northwest region of the United States in 1952. It was theorized that vegetative fragments or seeds of this seagrass were carried either by ballast water or in oyster (*Crassostrea gigas*) crates when these oysters were imported from Japan early in the 20th Century (Harrison and Bigley, 1982). The exact point of entry is a matter of speculation, but the distribution of *Z. japonica* is now widespread in the region with substantial populations at several sites around southern British Columbia in Canada, Washington State, and Oregon (Wyllie-Echeverria and Ackerman, 2003). The State of Washington protects *Z japonica* as a priority habitat (Pawlak, 1994) while the State of California, after finding a population in Humboldt Bay (40.47 N; 124.09 W) in the summer of 2002, executed a plan of eradication without conducting a risk analysis of secondary impacts (personal communication, Susan McBride California Sea Grant Program, Eureka, CA). Where it occurs, *Z. japonica* has changed the physical nature of the habitat and the density and richness of the indigenous fauna (Posey, 1988). Baldwin and Lovvorn (1994) describe the importance of these plants for herbivorous dabbling ducks (e.g. *Anas americana*, *A. acuta*) and brant geese (*Branta bernicla*), so whether this invasion warrants eradication is still subject to debate; calling into question any program of removal that could affect the overall biodiversity of the community.

Reproductively viable populations of another seagrass, *Halophila stipulacea*, migrated into the Mediterranean from the Red Sea, following the opening of Suez Canal, and has moved as far east as Italy (Lipkin, 1975; Boudouresque and Verlaque, 2002). Introduction and dispersal were thought to occur by vessels; however, this has not been verified. The recent report of *H. stipulacea* in the tropical west Atlantic (Ruiz and Ballantine, 2004) suggests the potential for long-distance introduction of some species. Although there could be numerous mechanisms of seagrass introductions, our knowledge of the transport vectors for any seagrass dispersal is minimal (Philbrick and Les, 1996; Waycott and Barnes, 2001).

Neither of these seagrass invasions suggests that non-native species can displace indigenous seagrasses; however, recent molecular studies with *Thalassia testudinum* indicate that even the slowest growing climax species can disperse long distances (Waycott and Barnes, 2001). They found representatives of the same individuals in populations on the Caribbean Coast of Panama and at the very northern limits of the species' geographic range in Bermuda. They hypothesized that since the last retreat of sea-level associated with the most recent glacial event 10,000 years ago, *T. testudinum* must have re-occupied a large portion of its original range in the Caribbean basin. The surviving source populations must have been located in deeper water refuges and were dispersed by currents, either vegetatively or by sexual propagules (Kaldy and Dunton, 1999; Whitfield et al., 2004). Assuming it was present prior to the last retreat of sea-level, *T. testudinum* was able to disperse back into its normal thermal range with the increased sea level. These observations, and reports of the recent spread globally *Halophila decipiens*, suggest that seagrasses have the capability to disperse long distances and interact with non-indigenous species (Waycott et al., 2002). The successful introduction and clonal spread of a dominant species like *T. testudinum* could result in the invasion of a superior clone that slowly displaces local populations. A critical need in seagrass conservation science is to link studies of genetic diversity with life history traits and experimentation on seagrass dispersal and competition so that we can better predict the outcome of an invasion (Waycott, 2000; see also Waycott et al., Chapter 2).

C. Scientific Disciplines and Research Priorities

1. Species and Population Level Science

Although conservation efforts in general are beginning to focus more on integrated landscape scale studies of systems and entire biomes, rather than on single species, there is a need to understand the biology and ecology of individual seagrass species and their populations. There are two important reasons for this. First, single species stands or stands dominated by a few species are common (Fig. 2: Duarte, 2000). Consequently, the interaction between ramets or genets within the same species, or plants from as few as two or three other species, is a common feature of the seagrass system. Second, community and biome level instruments of protection (e.g. light thresholds and nutrient criteria) are largely based on the understanding of individual species responses to environmental and anthropogenic stressors (Ralph et al., Chapter 24). Preventing the decline or extinction of seagrasses will be improved with a better understanding of individual species living requirements balanced by knowledge of community interactions and competition between species.

At the species and population levels, life history dynamics, dispersal, and genetics are among some of the most important scientific topics pertaining to the conservation of seagrasses (Philbrick and Les, 1996; Kenworthy, 2000; Waycott, 2000; Reusch, 2001). The common denominator for all these subjects is the question of population stability. Surprisingly, the least understood aspect of seagrass life history is the role of sexual reproduction including seed production, dispersal, and the survival and autecology of seedlings (Churchill, 1991; Terrados, 1993; Orth et al., 1994; Philbrick and Les, 1996; Inglis, 2000a; Orth et al., 2000; Kenworthy, 2000; Orth et al., 2003; Wyllie-Echeverria et al., 2003; Whitfield et al., 2004; Ackerman, Chapter 4; Orth et al., Chapter 5). A combination of clonal spread, seed rain, seed banks, and methods of sexual and vegetative dispersal enables these plants to survive, disperse and re-establish their populations (Duarte and Sand-Jensen, 1990; Duarte et al., 1994; Marbà and Duarte, 1998; Kenworthy and Schwarzschild, 1998; Harwell and Orth, 2002). Still, we do not know what constitutes an effective population size for maintaining individual species or what constitutes a seagrass metapopulation? For most seagrass species these subjects are poorly understood, a factor that continues to handicap our understanding of the population biology of clonal plants in general, and seagrasses in particular (Waycott, 2000; Duarte et al., Chapter 11). These are research topic areas where botanists, ecologists, molecular biologists, and modelers can interact to develop the appropriate structure and scale of predictive seagrass population models.

In the last decade the application of concepts derived from the clonal biology of terrestrial angiosperms to seagrasses has begun to advance scientific understanding of seagrass clonal systems (de Kroon and Groenendael, 1997; Duarte et al., 1994; Philbrick and Les, 1996; Terrados et al., 1997; Kenworthy and Schwartzschild, 1998, Marbà and Duarte, 1998). Investigations related to plant demography, including age structure of discrete cohorts and natality and mortality rates can be used to detect whether a population is in equilibrium, growing, or in danger of declining (Duarte and Sand Jensen, 1990; Duarte et al., 1994; Durako, 1994; Kenworthy and Schwarzschild, 1998; Marbà et al., 1996; Peterson and Fourqurean, 2001). This should continue to be a basic focus of research, because demography and life history processes will form the basis of models to predict seagrass recovery from disturbance and the benefits of conservation and restoration (Kenworthy, 2000; Fonseca et al., 2000b; Fonseca et al., 2002b; Fonseca et al., 2004).

2. Community and Ecosystem Level Science

Species exist in functional communities interacting with their environment and with other species, so it is not surprising that the preservation of intact biological communities is one of the most effective ways of conserving overall biological diversity (Duarte, 2000; Primack, 2000). Seagrasses have co-evolved among other coastal marine biomes and habitats such as corals, mangroves, and marshes and the flora and fauna in these biomes are complex and dynamic, moving among and between the different biomes at various life stages. The science of communities, ecosystems and biomes is central to the conservation of biodiversity, but this is more uncertain than targeting individual species dynamics (e.g. Bell and Westoby, 1986). Numerous papers discuss the topic of what constitutes a seagrass community but there needs to be greater attention paid to understanding the physico-chemical and biological processes which maintain the integrity of the communities and their function and stability in the biomes (Howard et al., 1989; Heck et al., 1995; Beck et al., 2001).

IV. Science-Based Protection Approaches

A. Overall Approach

The framework for implementing seagrass biome conservation can be attained through the general application of two approaches: (i) statutory authority (prescriptive) and (ii) general consensus planning (nonprescriptive), or a combination of the two (Coles and Fortes, 2001). Research supporting any one of these approaches or integrating studies that support some combination of these approaches can help managers develop tools for implementing conservation practices. Examples of the role of science in guiding the direction of these approaches follow.

B. Science and Prescriptive Approaches

Rarely are marine scientists given the opportunity to participate directly in writing statutes or legislation; however, indirect consultation with the scientific community as policies and programs develop often occurs and there are numerous examples of scientists making significant contributions to the development and implementation of laws for seagrass protection and conservation (Stephan and Bigford, 1997; Coles and Fortes, 2001; RAC-SPA, 2000). Even with the uncertainties associated with limited data and rapid response times, scientists can help managers make wise decisions without sacrificing scientific quality. Better known as adaptive management practices, scientists are frequently called upon to support difficult management decisions. For example, when a species is listed as either endangered or threatened under the United States Endangered Species Act a recovery plan must be formulated that includes identification of ‘critical habitat’. This statutory obligation requires scientific support for the selection of sites to be designated critical habitat. Because critical habitat provides a higher degree of protection for a species, the designations are often controversial. In the case of the threatened seagrass *Halophila johnsonii*, the first seagrass listed under the U.S. Endangered Species Act, critical habitat selection was one of the most contentious aspects of the listing process. Even so, the designated areas were supported by the available scientific data (National Marine Fisheries Service 2001; Recovery Plan for Johnson's Seagrass, *Halophila johnsonii*).

Direct protection by law or decree is most successful where there is adequate enforcement, widespread community support, and where scientific information supports the statutes. There are many examples where scientists are either tasked by agencies or voluntarily participate in conducting applied research in direct support of the designated rules or laws (Homziak et al., 1982; Fonseca et al., 2002a; Kenworthy et al., 2002; Orth et al., 2002; Whitfield et al., 2002). In developed countries like Australia, New Zealand, Japan, the United States, and the European Union Coastal States, government and non-government scientists formally participate in the process of reviewing and recommending actions pertaining to permits for development in the coastal zone as mandated by several statutes (Stephan and Bigford, 1997; Coles and Fortes, 2001). These countries have legislation requiring permits where damage to seagrass is likely, but the process is controversial, and decisions sometimes result in a net loss of habitat, even when there is every attempt made to avoid, minimize, and mitigate damages after project approval. The cumulative impacts of this approach can result in the degradation of seagrass biomes on both local and regional scales. One of the most challenging and critical areas of applied science is detecting and monitoring subtle cumulative impacts, determining the scale at which these are affecting entire systems, and either influencing modification to the regulations, or the development of new regulations to reverse the trend of cumulative effects.

Several Mediterranean countries are establishing specific legislative measures for seagrass protection backed by science. For instance, *Posidonia oceanica* and *Cymodocea nodosa* are directly protected by law in France and Spain and other examples include, (1) The Directive 'Habitat-Faune-Flore' edited in 1992 by the European Commission and (2) The Action Plan for the Conservation of Marine Vegetation in the Mediterranean Sea, adopted in 1999 within the framework of the Mediterranean Action Plan (UNEP) by all Mediterranean countries (RAC-SPA, 2000).

To expand the role of science in conservation, research is also needed to support and implement laws not directly safeguarding seagrasses but conserving them indirectly by: (1) protecting other organisms such as fish (e.g. Essential Fish Habitat or Fish Habitat Areas (Fluharty, 2000)), Special Area Management in Malaysia (Nickerson-Tietze, 2000) or protection of wildlife (e.g. US Endangered Species Act or IUCN Red List), (2) ensuring the quality of habitats within which seagrasses exist (e.g. U.S. Coastal Zone Management and Clean Water Acts), and (3) preventing known or recently discovered threats (e.g. legislation forbidding the import of exotic non-native species). These approaches must synthesize information from many disciplines and require the power of predictive models to forecast the consequences of 'no action' alternatives. Such approaches can have a significant positive impact on seagrass conservation, provided the scientific information can be translated into effective and reasonable habitat and biome conservation policies.

There are several examples where scientists actively participate in these processes. In the U.S., Fisheries Management Plans (FMP) must be accompanied by designations of essential fish habitat (EFH) which link critical life stages and trophic interactions of fisheries with the seagrass biome (Fluharty, 2000). The FMPs are prepared with input from a range of disciplines including but not limited to, biology, economics, and sociology and require the consensus of a panel (Marine Fisheries Commission) reviewing both the scientific data as well as the socio-economic factors. A similar program occurs in Queensland, Australia with the designation of Fish Habitat Areas (FHA). These particular examples and any future scientific contributions affecting seagrass conservation are going to be very important because one of the recognized issues in marine conservation are problems associated with over-exploitation of fisheries and fishing gear impacts to habitat, including seagrasses and associated communities (Peterson et al., 1987; De Jonge and De Jonge, 1992; Jackson et al., 2001; Orth et al., 2002). These are issues of community and ecosystem level science, because research indicates that over-exploitation in fisheries leads to a cascade of effects beyond just the top level predators or the keystone species (Beck et al., 2001; Heck and Orth, Chapter 22). In some instances, over-exploitation or habitat removal leads to shifts in productivity and community biodiversity. Attention to these topics will be especially important in developing countries where seagrass biomes are not yet damaged excessively by human activities but are under increasing threat due to the lack of control over activities that threaten this biome (Coles and Fortes, 2001; Lee Long and Thom, 2001; Green and Short, 2003).

C. Science and Non-prescriptive Approaches

Other effective conservation approaches outside of local, regional, and federal laws include legislatively required management plans that fuse prescriptive and non-prescriptive approaches. Non-prescriptive protection often relies on educational and informational outreach programs involving local citizens, commercial, and industrial stakeholders and NGO sponsored programs. Scientists should be encouraged to participate in outreach programs and partner with trained professionals knowledgeable in the preparation and presentation of information for use by public and private sectors to generate scientifically based conservation programs. In this dialogue scientists are challenged to discuss ecosystem principles with a wide range of participants whose experience in technical scientific issues may be very limited. To make substantial contributions to this process scientists must be capable of providing a clear interpretation of sophisticated and complex technical information.

Perhaps the most controversial yet promising conservation tool is the design, planning and implementation of Marine Protected Areas (IUNC, 1994; Lubchenco et al., 2003). Many areas around the globe exist as protected areas by default simply because human habitation has not reached a level that is damaging. These locations need to be identified and evaluated to determine the necessary balance between conservation programs and traditional use before the advances of industrial society are exported to pristine sites (e.g. Cox and Elmqvist, 1993). Of the estimated 4,000 MPA worldwide 247 are known to contain seagrasses (Green and Short, 2003). The two largest seagrass protection areas in the world occur in two MPAs, Australia's Great Barrier Reef Marine Park (GBRMP) (Coles et al., 2000) and in the United States in the Florida Keys National Marine Sanctuary (Fourqurean et al., 2001). These are the two most high-profile examples of seagrass protection on a scale large enough to have regional implications for conservation; however, few MPAs have been designated with adequate scientific input to achieve the appropriate boundaries and sizes (Jameson et al., 2002). The slow development of MPAs is partly due to socio-political misunderstanding, cost, and inadequate administrative support, especially in the developing world (Coles and Fortes, 2001). Yet, this should not deter future efforts to redirect scientific resources toward developing nations where the potential for conservation of as yet undamaged resources is enormous and the pressure for economic development and population growth is an even greater threat to existing biodiversity.

V. Implementing Conservation Tools: Two Examples

We conclude with two examples illustrating the utility of a conservation biology approach to protect seagrasses. The first example is a program that develops water quality criteria for seagrass conservation in a large estuary in the mid Atlantic region of the United States. In the second example, taken from recent experience in Australia, we illustrate the process of establishing a wider scope of protection for seagrasses in the Marine Protected Area of the GBRMP.

A. Chesapeake Bay Seagrass Conservation and Water Quality Criteria Development

1. Water Quality Management

Vital to the success of any coastal marine conservation effort is the maintenance and improvement of appropriate water quality standards for seagrass flora and fauna (Kenworthy and Haunert, 1991; Dennison et al., 1993). One of the best examples of this is the Chesapeake Bay, the largest estuary in the U.S., where scientists, managers and the public have collaborated to conserve seagrasses through water quality criteria and protection (Dennison et al., 1993; Batiuk et al., 2000). Here a species level basic research program, focused on the physiology and autecology of seagrasses (*Zostera marina* and *Ruppia maritima*) and other submerged aquatic vegetation, incorporated geographic information on recent and historical seagrass distributions using remote sensing technology, integrated these maps with bathymetry measurements and water quality data, and developed a model to predict the presence of seagrass under a combination of water quality scenarios (Dennison et al., 1993; Batiuk et al., 2000). Basic process-oriented research was combined with a mapping and modeling research program to develop conservation goals for seagrasses. The program responded to a crisis of seagrass loss by organizing human resources, setting a clear and concise goal for expected distribution and abundance of seagrass communities, and developed a model that predicted environmental criteria necessary for seagrass survival. Performance measures were assessed by monitoring the response of seagrass distribution to water quality conditions. For the very first time in the U.S. the designated criteria for seagrass growth and survival were driving the actions necessary to manage nutrient and sediment loadings in the watershed. Also included in these criteria were parameters that affected other community components, such as fish (i.e. dissolved O_2) and plankton (i.e. chlorophyll a), directly linking seagrasses to other important resources within the framework of the Bay-wide ecosystem criteria. Faunal community components depending on seagrass habitat (e.g. fish and shellfish) were identified by the social and economic needs of the Bay residents as vital to the health and well-being of the seagrass biome and economy of the Bay. At the same time, the scientists met with resource managers from several state jurisdictions and encouraged them to adopt the criteria.

2. Developing Metrics of Seagrass Systems

Evaluation of community level performance measures that address the biodiversity of seagrass ecosystems requires a great deal of time-consuming and expensive monitoring. Recently, scientists involved in ecosystem level research in seagrass systems have suggested that we can utilize reasonably simple metrics of dominant community types to act as surrogates for habitat quality, community composition, and ecological services (Dennison et al., 1993; Fonseca et al., 2000; 2002). For example, something as simple as a visual estimate of seagrass cover and the maximum depth to which seagrasses grow may be adequate to predict the seagrass community response to improved water quality. The difficult process of articulating the scope of resource services into simple metrics is one aspect of seagrass science that must be effectively translated for managers and the public for support of conservation efforts. If it is possible to collapse many services into one or a few metrics, the cost of monitoring and protection could be greatly reduced. The appropriate scaling of functions and services is an important area of future research. Time, personnel, and budget constraints demand the selection of functional indices in system-wide monitoring programs designed to identify responses to threats, areas for protection, and the performance of protected areas recommended by managers. We need quantifiable metrics that address community composition and dynamics but are easily measured, repeatable, and can be transferred between geographic locations, systems and even biomes (e.g. Neckles, 1994; Fonseca et al., 2000a).

In the Chesapeake Bay program the metric was defined by seagrass cover to a specified water depth. Seagrasses and freshwater angiosperms were, as suggested by Dennison et al. (1993), the ‘canaries in the mine’; in this instance the mine is the estuary and the seagrasses are signaling the health of the water body. Future expectations were developed from an historical data set of seagrass distribution and predictions of the outcome of various management options were made with an optical water quality model, which identified the environmental conditions permitting the seagrass distribution. The example in the Chesapeake Bay is a new approach to setting water quality criteria where the target community drives the criteria and not the inverse, which was the usual case for setting standards (Kenworthy and Haunert, 1991; Dennison et al., 1993; Gallegos and Kenworthy, 1996; Gallegos, 2001). At the time the Chesapeake Bay program started, existing water quality criteria were set without detailed empirical information or synthesis and were based on the requirements of freshwater SAV and plankton and were inadequate for seagrass protection (Kenworthy and Haunert, 1991). The Chesapeake Bay example illustrates the possibilities that can be realized through collaboration across scientific disciplines and cooperation between stakeholders across jurisdictional boundaries (Batiuk et al., 2000). The dialog between scientists and managers continues, the criteria are improving, and overall, the program is a good example of adaptive management for seagrass conservation in developed countries. For future application of this approach in developing regions, scientists and managers will have to initiate monitoring and resource inventory programs located in remote areas that will have to depend on innovative techniques, remote sensing technologies and indigenous populations to gather the information and implement the conservation programs necessary to protect seagrasses: a challenging but necessary scientific endeavor.

B. The Great Barrier Reef: A Representative Areas Approach for Protecting Biodiversity Including Seagrasses

1. The Great Barrier Reef Marine Park

Establishing Marine Protected Areas requires careful definition of the location, size, and comprehensive representation of species, habitats, and ecosystems representative of the biomes protected by the MPA (Jameson et al., 2002; Lubchenco et al., 2003). The Great Barrier Reef World Heritage Area in northeastern Australia is the largest world heritage site covering 347,800 km^2 and stretching along approximately 2,000 km of coastline in northeastern Australia. It is managed as part of a very large MPA—the Great Barrier Reef Marine Park. Although it is best known for its approximately 2,800 coral reefs, coral accounts for only about 6% of the total area. Inter-reef and lagoon areas are far larger at 61%, with the continental shelf making up the balance of the area (Lee Long and Thom, 2001; Wachenfeld et al., 1998). It is also one of the most important sites in Australia for seagrass biodiversity, with 15 species. Nearly 6,000 km^2 of seagrass beds grow in water shallower than 15 m and as much as 40,000 km^2 of seagrass occur in waters deeper than 15 m (Coles et al., 2000). The GBR is typical of a vast biome of seagrasses found throughout the Indo Pacific region and conservation practices in the GBRMP are a model applicable to other sites in the region as well as other locations.

When the Great Barrier Reef Marine Park was established in 1975 it was designed to protect coral reefs and minimize conflict between users. In highly protected areas nonreef habitats were severely under represented, including seagrasses. Since 1975 scientific understanding of the significance of interconnectivity across reef and nonreef areas and the concepts of ecosystem services and protection of biodiversity have radically changed protected area management approaches. A review of existing zoning arrangements in the GBR, recently concluded, has used an approach that identifies and protects representative examples of the biodiversity of habitats and processes upon which species depend rather than focusing on individual species or specific habitats. A representative area is defined as an area that is typical of the surrounding habitats or ecosystems at a selected scale (GBRMPA, 1999). This Representative Area Program approach is a departure from the past of protecting parts of the Marine Park perceived to have a high value, to protecting a range of habitats that are representative of the biodiversity in the area. Some areas included in a representative approach will not be perceived by others, such as fisheries agencies and public users of the reef, to have a high conservation value, yet may exclude them from some activities in those areas.

To implement a Representative Area Approach over such a large region a biophysical analysis was guided by an independent scientific steering committee with an analytical working group providing modeling, statistical analysis, GIS skills, and general guidance. This process provided conservation options that were then refined using socio-economic data and expertise followed by a formal statutory process which included public consultation. The three-step process is outlined in Fig. 7. In the classification phase a biological conservation approach was implemented in two ways. Knowledge was collected by interviews from over 60 experts, most with scientific expertise, including indigenous and fishing industry people. This "Delphic"-type approach was combined with about 60 key biophysical data sets (e.g. seagrass, algae and bottom community, geomorphology, topography, and oceanography) and with data on special and unique areas in an interactive workshop with GIS overlays and analysis. From this, 70 bioregions were identified. A bioregion was defined as an area within which habitats, communities (areas such as seagrass) and physical features (such as sediment and water depth) would be more similar to each other than to similar habitats (or communities) occurring in other bioregions (Day et al., 2000). This process provided a conceptual approach to understand the heterogeneity of this large system and the basis for designing a reserve network system—a part of each bioregion would be included for protection.

2. Highly Protected or No-take Areas

The second phase of selection used the bioregions and scientific data to select various options for including parts of the Marine Park in highly protected areas or no-take areas. The identification process used a modified reserve design software program MARXAN based on the terrestrial SPEXAN (Ball and Possingham, 2000), and other tailored analytical tools (De'arth and Fabricius, 2000). If several configurations of highly protected areas exist that satisfy

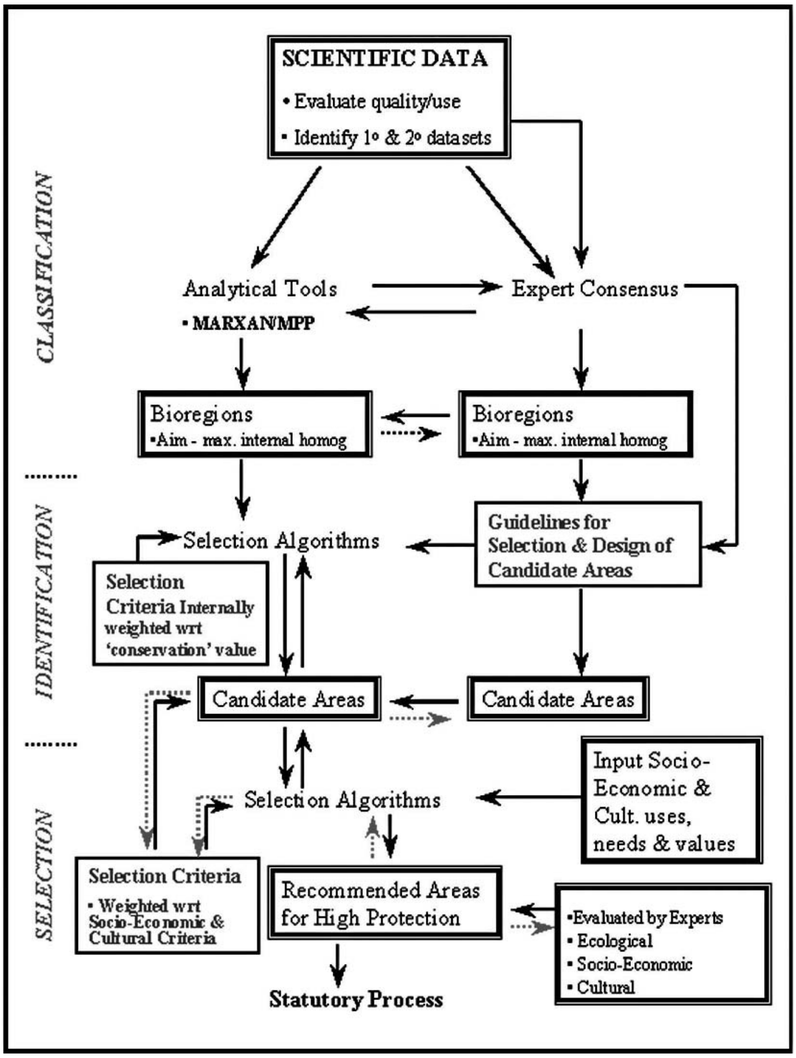


Fig. 7. Flow diagram illustrating the process for selecting representative conservation areas in the Great Barrier Reef World Heritage Area (From a presentation by Leanne Fernandes (2001) for the Great Barrier Reef Marine Park Authority).

conservation biology strategies, then an option that provides the most benefit to conserving biodiversity with the least cost to existing activities can be selected. Some habitat types may be protected equally well at several alternative locations. Solutions developed by the reserve design software that satisfied eleven biophysical principles were then redesigned subject to socio-economic principles and data to develop a reserve system with the least impact on existing commercial and recreational activity (Table 1; and see Day et al., 2000 and http://gbrmpa.org.au for a full description). The socio-economic principles included: (1) maximize complementarities of no-take areas with human values, activities, and opportunities, (2) ensure that final selection of no-take areas recognizes social costs and benefits, (3) maximize placement of no-take areas in locations which complement existing or proposed zoning, management plans and tenure of managed coastal areas, and (4) maximize public understanding and acceptance of no-take areas as far as possible with simple shapes, easily identified boundaries and with fewer large areas rather than more smaller areas.

3. Protecting Seagrass Systems

The current program represents a significant shift from the principles used in the original Marine Park

Table 1. General principles guiding the size of no-take areas within the Great Barrier Reef Marine Park.

1 *Have no-take areas the minimum size of which is 20 km along the smallest dimension:* This approach provides for the maintenance of populations of plants and animals, reduces edge effects and allows for easier enforcement.

2 *Have larger versus smaller no-take areas:* This configuration minimizes edge effects from surrounding usage and insures greater connectivity.

3 *Have sufficient no-take zones to insure against negative impacts on some part of a bioregion:* Three to four no-take zones were considered adequate for most bioregions to ensure against impacts such as an oil spill or tropical storm.

4 *Where a reef is incorporated into no-take areas the whole reef should be included:* Reefs of the Great Barrier Reef Marine Park include habitats such as coral, sand lagoons and lagoon and reef platform seagrass meadows and are relatively integral biological units with a high level of connectivity.

5 *Represent a minimum amount of each bioregion in no-take areas:* In most non reef bioregions this amount was set at 20%, a so called ecological bottom line below which a consensus of the scientific steering committee felt the marine park would not be adequately protected (present solutions to the reserve modeling are running between 20 and 30%).

6 *Recognize cross-shelf and latitudinal diversity in the network of no-take areas:* This approach recognizes that processes that sustain the ecosystems of the Great Barrier Reef maintain connectivity with the adjacent coast which is important for migratory fish and for seagrasses which extend from estuaries out to 60 m deep in this region.

7 *Represent a minimum amount of each community type and physical environment type in the overall network:* Scientific consensus set sizes at 10% of all shallow water seagrasses and 10% of all deep water seagrasses (and 10% of algae and *Halimeda* beds). In addition to establishing the size of seagrass biomes the model was asked to find solutions that included defined amounts of all identified habitat types for which a data set existed.

8 *Maximize use of environmental information to determine the configuration of no-take areas to form viable networks:* The design of spatial configurations of no-take areas developed by the reserve software was asked to include information on connectivity, migration and issues of sink/source interactions with the recognition that for much of the area and for habitats such as seagrass this information is generally unavailable.

9 *Include biophysically special and unique places:* The model was asked to include as many identified special and unique places as possible including areas of seagrass identified in Dugong protected areas and a small site where an unusual morphology of *Halophila* spp. is found.

10 *Include consideration of sea and adjacent land uses in determining no-take areas:* Locating reserve areas adjacent to terrestrial parks or areas of low human impact was considered desirable as was using existing highly protected areas included in the existing management scheme.

planning that took place in the early 1980s. At that time the opinion of 'experts' gave far more weight to areas thought to have special values or to be pristine and these were included in highly protected zones. The concept of protecting biodiversity in seagrass meadows and open sand banks within the Marine Park received little consideration. Charismatic sites such as attractive coral reefs and areas with complex fish populations were selected; connectivity was considered with a cross shelf transect but this was located in a remote northern region of the park where at the time little biophysical information was available and it was assumed impacts from human activity were minimal. Little consideration was given to ease of enforcement.

The key changes in approach have been the increases in biophysical knowledge about the Marine Park environment, particularly inter-reef habitats such as seagrasses and algae beds. Better information on the scale of processes such as fish and coral spawning and water current modeling give a much better idea of connectivity. Databases from fishing activities are now readily available particularly with the trawler fleet using a real time electronic monitoring system.

An important gap, especially for seagrasses, is that no-take zones or any highly protected spatial design to protect important habitat types must also include some management of adjacent coastal activities. With high levels of pesticides measured from inshore seagrass meadows and sediments in the Marine Park (Preen et al.,1995; Haynes et al., 1999) that are likely to come from agriculture, this is easily as important as the physical threats from trawling or tropical storms. Concern about the effects of land uses are being addressed through a separate cooperative approach among landholders, the Queensland State Government, and the GBRMP Authority.

But most important in this process has been recognition of a broader understanding of the intrinsic value of biodiversity in the marine environment. With the availability of sophisticated computer models to analyze complex data guided by a set of principals or conditions, marine park managers and users of the area have demonstrated a willingness to enter into constructive negotiations to find an acceptable network of highly protected or no-take zones, representing about 25% of the total area of the GBR, the to ensure the long-term conservation of species and habitats, including seagrasses.

VI. Summary and Outlook

The geographic and temporal scale of these two examples illustrates that science-based strategies can significantly influence and determine the success of seagrass conservation programs. It is clear that these approaches to conservation can be applied to other locations but with some caution. We say "caution" because application of a conservation biology perspective in terrestrial ecosystems teaches the importance of recognizing the biological and cultural uniqueness of each bioregion—what fits one place may fit another only with alteration. This concept may run at cross-purposes to traditional ecological theories (i.e. generalized rules apply generally), but it is in keeping with the complex dynamic of local and regional blends of biology, ecology, physicochemical properties and culture exposed by a conservation biology perspective. The importance of this paradigm shift cannot be undervalued because the goals and objectives of conservation biology, in addition to protecting biodiversity, are to support and encourage sustainable programs with respect to resource extraction and to encourage humans to recognize that services provided by natural systems control the quality of life for all species. While this approach is in conflict with cost benefit analysis in the short-term—"give me (us) what I (we) want now"—the long term survival of humans and the natural systems, which drive the biochemical and physical forces that shape cultures and societies, depend on our willingness to acknowledge the prudence of long-term thinking.

Having said this, we recognize that evolution is a dynamic process punctuated by events that cannot be fully explained or controlled by humans. Evolution within the seagrass biome and the seagrasses themselves conforms to this process—there was a time before seagrass and there may be a time in the future when these plants are ancient ancestors of new floral assemblages. However, rapid rates of species extinction and destruction of habitat directly linked to human activity are unacceptable. We have pointed out the vital importance of the seagrass biome not only for services that nourish and support human cultures but also the strong link between the health of this biome and nearshore and estuarine productivity and biodiversity. Our selective review of the literature through the lens of a conservation biology perspective convinces us that insights of this discipline are necessary to arrest the global trend of seagrass loss. As Duarte (1999) pointed out, deficiencies in our understanding of seagrass biomes sharply curtails our ability to predict the consequences of seagrass loss and this is largely due to the fragmented nature of the research community. Conservation biology of seagrasses can serve as a focal point for synthesis of disciplines and ultimately for the advancement of understanding and at the same time serve as a tool for future protection.

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Chapter 26

Seagrass Ecology: New Contributions from a Landscape Perspective

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I. Introduction

Landscape ecology is the study of processes occurring across spatially heterogeneous mosaics and the biotic responses to the resulting pattern. Spatial mosaics are made up of structural elements, biotic, and/or abiotic, which produce a set of patches set in a homogeneous matrix. Quantitative analyses of spatial and temporal patterns resulting from patch dynamics form the basis of landscape ecology. A landscape is larger than an individual's immediately observable area (Allen, 1998) and landscape studies typically address heterogeneity at very large spatial scales relative to the organism or process of interest.

While terrestrial ecology has been studied at the landscape level for several decades, only more recently has the explicit examination of patch dynamics and spatial arrangement been applied to the study of seagrasses in the marine environment. Studies of marine landscapes are not limited to seagrasses: application of this approach to soft sediment systems (Zajac et al., 2000) and salt marshes (Costanza et al., 1990) has also been documented. Given that seagrasses represent a group of over 60 species worldwide (den Hartog, 1970; den Hartog and Kuo, Chapter 1) and cover extensive areas of coastal sub-tidal habitats (e.g. Fig. 1), they are appropriate for study using a landscape approach. Additionally reader will find reference to this subject in several other chapters in this book, e.g. Valentine and Duffy, Chapter 20; Kenworthy et al., Chapter 25.

The idea of applying landscape analysis to seagrasses was formally presented by Robbins and Bell (1994). Although an intervening layer of seawater makes the most common sources of data in terrestrial landscape studies (aerial photography and remote sensing) more complicated to analyze for seagrass systems (see Dekker et al., Chapter 15), Robbins and Bell (1994) argued that a landscape approach could nevertheless be quite valuable. Landscape studies can address questions of scale and fragmentation in seagrass beds, and once established, the approach could potentially be applied to other marine and aquatic systems (Robbins and Bell, 1994) and even restoration efforts (Fonseca et al., 1998; Bell et al., 1999). Virnstein (1995) also recommended the application of landscape ecology (e.g. a large scale approach) to improve management of seagrass habitat diversity in the Indian River Lagoon (Florida).

In this chapter, we provide first a brief review of concepts and techniques associated with a landscape

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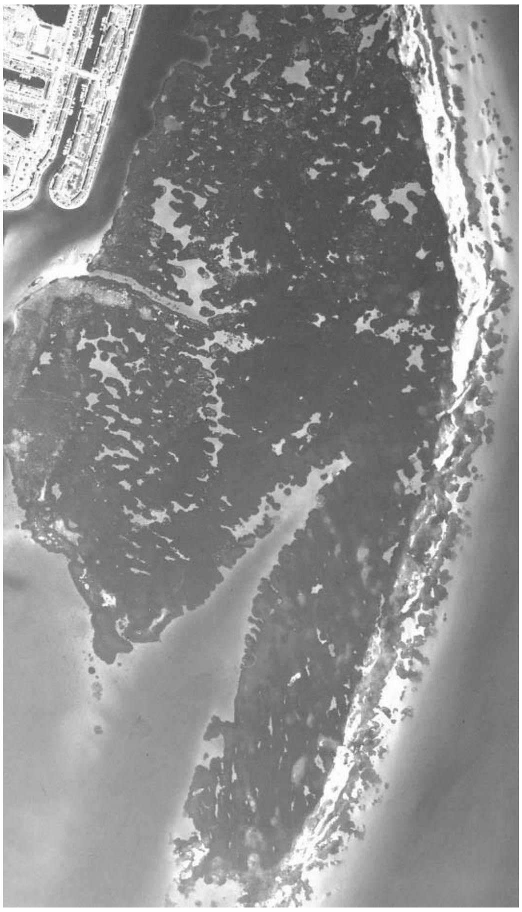

Fig. 1. An example of a seagrass landscape located in Tampa Bay, Florida, USA. Clearly evident are seagrass patches of variable size (dark areas) on the open-water side of the shoal, while larger, contiguous patches are interspersed with unvegetated gaps shoreward of the shoal. Image is taken from a 1993 photograph provided by the Southwest Florida Water Management District.

approach. Next we review the literature that has discussed various topics related to landscape ecology of seagrasses. We also evaluate how information collected from studies in seagrass systems compares to that from analogous terrestrial systems/landscapes. Finally, we discuss some potential areas of future research in the field of seagrass landscape ecology, recommending conceptual, and methodological improvements.

II. The Landscape Approach

Landscape ecology of seagrass beds has focused on spatial configuration of patches, as patches represent the elementary component of landscape shape and dimension (Farina, 1998). Stine and Hunsaker (2001) defined patches as areas: (1) displaying relative homogeneity with respect to some property at a particular scale, and (2) exhibiting a relatively abrupt boundary to adjacent areas of different quality. Likewise, landscapes may be composed of a single patch type, but often more than one patch type may be present (see Fig. 2).

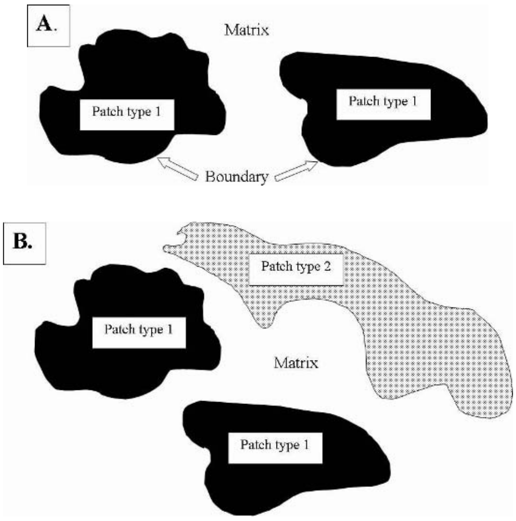

Fig. 2. The components of a landscape study. **A**. Patches of the same type reside within a matrix and boundaries exist between patches and the matrix. An example of this would be seagrass patches and sedimentary matrix. **B.** As in '**A**' but with two different kinds of patches. An example of this would be seagrass and macroalgal patches within a sedimentary matrix.

The quantitative analysis of temporal and spatial patterns formed by patches and the matrix within which they reside utilizes a number of unique quantitative metrics. A representative group is presented in Table 1. These metrics can be determined for seagrass landscapes if appropriate spatial information on seagrass vegetation is available. Such patch-based analyses of seagrasses provide an approach that is intuitively logical, amenable to interpretation, and relevant to ecological theory (see Gustafson, 1998). More importantly, these metrics provide a basis for quantitative comparison across landscapes.

The use of landscape metrics of course must be interpreted with respect to grain size and extent of data collection. Grain size (e.g. cell or pixel size in raster images) refers to the finest level of spatial resolution, while extent refers to the dimensions of the entire study area over which data were collected (see

Table 1. Landscape descriptors used in quantifying landscape elements [modified from Robbins and Bell (1994) and Gustafson (1998)].

Descriptor	Definition
Complexity	A measure of patch size and shape; an index based on the ratio of patch perimeter to area
Patch isolation	A measure of the distance between an individual patch and its nearest neighbors
Contiguity; contagion	A measure of patch aggregation or dispersion; the index is the inverse of a fragmentation index
Landscape diversity	A measure of the proportion of the landscape exhibiting a given element type
Landscape dominance	The proportion of an element type compared to all landscape elements
Fractal dimension (D)	A measure of boundary complexity; the calculated 'fractional dimension' indicates whether a boundary is closer to linear ($D = 1$) or approaches the second dimension ($D = 2$).

next section on scale). The extent and grain size of data used in analyses of landscape patterns have a strong effect on the values of the landscape metrics (Gergel and Turner, 2002). This is illustrated for a selected landscape in Fig. 3 and Table 2, which together demonstrate the effect of varying grain size on comparative landscape metrics. Clearly differences in resolution can make quantitative comparison of landscapes quite challenging.

So how should one select the appropriate grain size? The selection is linked to the ecological process of interest (e.g. the perceptual scale of a crab in a study of crab utilization of seagrass patches) and defines the maximum possible accuracy (Fortin and Edwards, 2001). In fact, this aspect of data quality may often be beyond the control of the investigator. Nonetheless, when grain size is too large spatial patterns of seagrasses can be obscured (e.g. a 10 m cell size in patchy seagrass with a mean patch diameter of 3 m). Conversely, investigations conducted within small, circumscribed extents may fail to detect landscape patterns or provide a meaningful inference scale (e.g. inferring seagrass landscape properties by sampling from a single 5×5 m^2 patch within a clearly delineated area of 10 m seagrass patches covering a hectare). Thus, both grain and extent are critical features of the design of (seagrass) landscape studies, although they are often

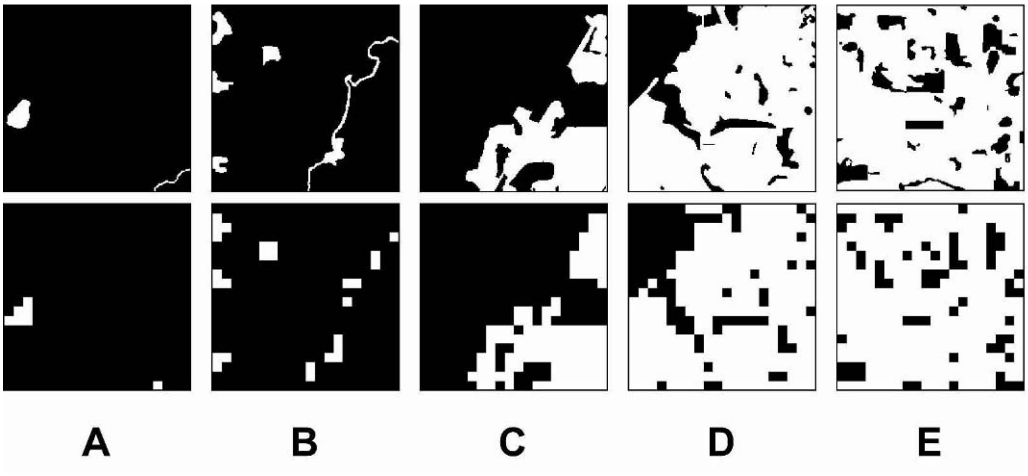

Fig. 3. The spatial arrangement of landscapes can be quantified by various metrics (see Table 1 for descriptions of some of the more common metrics). Five different rasters (A–E) representing a gradient of apparent fragmentation are shown (see Table 2 for sample landscape metrics), at each of two different resolutions [10 m (top) and 100 m (bottom) cells]. Landscapes were derived from the Southwest Florida Water Management District 1995 land use map of Tampa; each landscape is 4 km^2 in area.

Table 2. The values for selected metrics for the five landscapes (A–E) at each of two grid cell resolutions [10 (top) and 100 (bottom) m] from Fig. 3 calculated in ESRI's Arc View 3.3 using the Patch Analyst Extension. Analyses were conducted with an embedded version of FragStats (McGarigal and Marks 1995), a landscape analysis program. An 8-cell neighborhood was used by default, meaning that diagonally adjacent pixels are considered as contiguous. Note the sensitivity of many of the metrics to the input scale. Top—10 m resolution; Bottom—100 m resolution. N/A—not applicable. AW—Area Weighted; MSI—Mean Shape Index; D—fractal dimension; NN—Nearest Neighbor; PI—Proximity Index.

	A10	A100	B10	B100	C10	C100	D10	D100	E10	E100
Number of patches	2	1	3	1	11	4	28	15	33	20
Mean patch size	196.9	393.3	126.1	374	26.5	72.0	3.4	6.7	2.0	3.3
Total edge	10,400	9200	17,640	13,400	17,220	13,400	20,360	16,000	25,860	17,400
Edge density	26.4	23.4	46.6	35.8	59.0	46.5	213.7	160.0	390.1	267.7
AW MSI	1.17	1.16	1.63	1.73	1.75	1.58	1.97	1.95	1.74	1.33
AW mean patch *D*	1.02	1.02	1.07	1.07	1.08	1.06	1.11	1.10	1.10	1.05
Mean NN	10.0	N/A	23.3	N/A	37.5	100	100.9	147.9	77.0	158.5
Mean PI	19,684	N/A	12,974	N/A	357.4	97.5	116.6	15.6	89.2	4.9
Total core area	393.7	393	378.3	374	292.0	288.0	95.3	100	66.3	65.0
Mean core area	196.9	393.0	126.1	374.0	26.5	72.0	3.4	6.7	2.0	3.3
Core area density	0.5	0.3	0.8	0.3	3.8	1.4	29.4	15.0	49.8	30.8

established by logistical rather than purely analytical considerations.

A. Scale

The concept of scale as it pertains to landscape ecology merits particular discussion and is integral to both the theory and practice of landscape ecology. Scale, whether temporal or spatial, combines two components: extent and resolution (Schneider, 1994). Spatial scale is therefore composed of the actual size (extent) of the landscape of interest as interpreted by samples of a given grain size (resolution). These two components of scale must be considered simultaneously when comparing within and between landscapes. It is important to emphasize that the choice of scale in an investigation is one of the most crucial decisions that a researcher may make (Dayton and Tegner, 1984; Levin, 1992).

Although specifically addressed in some studies of community dynamics (e.g. Sousa, 1985), most work on the effects of spatial scale in ecology has been theoretical and focused on terrestrial settings. In one of the few papers where manipulative experiments have been conducted, Robinson et al. (1992) concluded that the spatial extent of vegetation impacted the distribution patterns of small mammals. In 1994 with employed a landscape approach, and found that the size of grasshoppers determined the spatial extent and resolution at which they perceived habitat heterogeneity. Additionally, Turner (1987), Turner and Gardner (1991), and Weins et al. (1993) reviewed the theoretical effects of spatial scale on ecological processes. Studies of the effects of spatial scale on seagrass experiments are almost non-existent.

Despite the widely acknowledged, critical nature of scale selection in both mensurative and manipulative experiments, the spatial extent of a study area and resolution of sampling within that area are often based on historical sampling conventions (e.g. 1 m^2 samples), intuition, and available data. Therefore, evaluation of ecological phenomena, such as species distribution and abundance, predation, competition, growth, and dispersal (all of which may vary with or are explicitly dependent upon spatial scale) have the potential to be biased, especially if historical sampling conventions were originally designed for different organisms or phenomena. For example, a methodology developed for the study of dugongs is likely to be inappropriate for a study of amphipods without careful correction for scale differences including the vastly different perceptual scales of the animals, the different relationship between body size and movement patterns, and so on. In addition, the initial choice of spatial scale may limit one's ability to detect local sources of variation because chosen metrics may or may not vary at that scale [see Robbins (1997) for a practical example of this issue for seagrasses].

In fact, confusion often arises at the mention of 'scale' because grain and extent are often not reported by researchers or because no distinction is made between the two components and only one value is reported. A study reporting crab behavior at a 1 m scale leaves the reader unclear on whether it is the grain size or the extent that is represented by 1 m. Besides the basic problem of differences in opinion on appropriate scale for an organism of study, the choice of scale in a study is, by default, autocorrelated with results. This intertwining of scale and results arises because of the simple premise that units of X become less similar as a function of distance or time that separates them. We generally recognize that a given unit X, when sampled over time, is not a replicate sample unless we invoke special tools for dealing with repeated measures; that is, the sample at time $(t + 1)$ is strongly influenced by the state of the unit at time (t) [i.e. they are autocorrelated, (Goodchild, 1987)]. What is often not addressed in ecological studies is that these same attributes apply to sampling units in space as well as time. For example, it is probable that two adjacent square metre plots of seagrass are more likely to be similar to each other than a comparison of two plots separated by 100 m. Therefore, resolution will influence observed variance between samples.

The notion that two units of seagrass have declining similarity as a function of distance has an important implication: if two samples are related as a function of distance apart, then samples taken too closely together are not independent, which violates most assumptions used in statistical analyses (Fonseca, 1996). Thus, the choice of spatial grain and extent may render invalid the apparent results because of spatial autocorrelation of data. Discussions of tools that can be employed to address such spatial autocorrelation of data are available in Cressie (1991) and Rossi et al. (1992), and these are useful general references for spatial analyses of seagrass landscapes.

III. Historical Overview

Here we survey the literature that has applied concepts of landscape ecology as presented above to seagrass ecosystems. Excluded from this historical overview are the many valuable studies reporting estimates of seagrass coverage and change, i.e. chronosequences (e.g. Orth and Moore, 1983; Pulich and White, 1991; Fletcher and Fletcher, 1995). Although many of these studies were done at or beyond what might be considered the landscape scale, by simply tracking changes in the areal extent of seagrass beds they do not specifically apply landscape theory or metrics to their analyses, and hence these studies will not be addressed here. The papers that do apply landscape theory to seagrasses fall largely into two groups: those that examine (1) factors that modify seagrass landscape structure and persistence, and (2) relationships between seagrass landscape characteristics and ecosystem components. We first review the papers dealing with seagrass vegetation as the primary patch type, and then discuss those that address how the size, shape, and arrangement of seagrass patches affect other ecosystem components.

A. Investigating Seagrass Landscapes

1. Patch Structure and Dynamics

The application of landscape principles to seagrass systems is well represented by studies attempting to quantify patch structure, arrangement, and dynamics of vegetation (see Duarte et al., Chapter 11 for a discussion of the clonal nature of seagrass beds to patch structure and dynamics). One of the first studies to take a landscape approach to seagrasses was that of Olesen and Sand-Jensen (1994), which examined the patch dynamics of *Zostera marina* in a semi-enclosed embayment in northern Denmark. Over 2.5 years a fringe of eelgrass patches bordering a continuous bed was studied (Olesen and Sand-Jensen, 1994). The authors reported that patch size was skewed toward smaller patches (50% were <2 m), but small, young patches were susceptible to a high mortality rate; lateral expansion rates of patch edges were not affected by patch size (Olesen and Sand-Jensen, 1994). In a similar study with somewhat contradictory results, Vidondo et al. (1997) found lateral expansion rates increased with size of *Cymodocea nodosa* patches in the Mediterranean. They noted the same predominance of small patch sizes and high rate of patch mortality as was reported for *Z. marina* in Denmark, but also found that rate of patch recruitment exceeded the high mortality rate (Vidondo et al., 1997). These studies advanced the concept that seagrass landscapes represent a level of organization and interaction beyond the spatial scale of individual clonal units.

Studies investigating temporal dynamics of seagrass patches have considered landscape level questions. A study of *Zostera novazelandica* patches by Ramage and Schiel (1999) in New Zealand tracked patch dynamics at the landscape scale and found patch expansion occurred primarily on the landward edge of the landscape. They also documented that experimental disturbance had greater impact on patch mortality when directed at the expanding landward edges of patches (Ramage and Schiel, 1999). In a study of *Halodule wrightii* patches on a shoal in Florida, USA, Jensen and Bell (2001) noted a correlation between belowground morphological characteristics and aboveground plant dynamics. They suggested that patch dynamics of seagrasses at the landscape scale might result from small-scale plastic behaviors of individual seagrass ramets. These studies offer some insight into how spatial arrangement of patches within a landscape may be dynamic and can potentially be influenced by a variety of factors.

One aspect of patch dynamics, which is of critical concern, is the origin of patches within a landscape. Several studies have examined the ability of seagrasses to colonize unvegetated areas. A possible source of new patches is from seed dispersal and successful plant germination (see Orth et al., Chapter 5). Orth et al. (1994) showed that *Z. marina* seeds were capable of only very limited dispersal under normal conditions, and argued that reliance on surviving patches to recolonize 'sink' populations of this species at even moderate distances was probably not feasible. In a review of seagrass seed dormancy, Orth et al. (2000) suggested that studies of seeds in a landscape context, such as a comparison of the spatial arrangement of the seed bank to the distribution of seagrass above it, would be instructive for evaluating the persistence of populations of this species [see also Inglis (2000)]. Hammerstrom and Kenworthy (2003) documented the existence of a seed bank for *Halophila decipiens* in offshore seagrass beds, which serves as the dominant mode of new patch origin (and therefore landscape spatial structure) in these coastal sediments on an annual basis.

2. Asexual Propagation and Faunal Interactions

Many studies on seagrass growth and/or reproduction suggest that local persistence and long distance dispersal of seagrasses are often achieved by asexual spreading via rhizome elongation rather than by seed recruitment (e.g. Marbà and Duarte, 1998; Rollon et al., 2003; Duarte et al., Chapter 11). However, information on the contribution of asexual reproduction of seagrasses to the development of new patches remains limited in scope. Robbins and Bell (2000) reported the appearance of new patches of *Halodule wrightii* over a 2-year period in FL, USA, and because seeds were never observed on plants at the site, concluded that these patches must have arisen from asexual growth alone.

Apart from sexual reproduction via seeds or asexual reproduction by clonal lateral growth, neither of which appear likely to foster dramatic recovery of many seagrass species into denuded areas, viable fragments of seagrass shoots transported over large distances remains the suggested mode of seagrass recruitment into unvegetated areas in some locations. Harwell and Orth (2001) reported that reproductive shoots of *Z. marina* were present in the tubes of 70% of the polychaete, *Diopatra cuprea,* examined in the Chesapeake Bay. If worms in unvegetated sediments can capture viable reproductive shoots, which then drop their seeds adjacent to the tubes, worms could perhaps be a catalyst for the colonization or recovery of seagrasses into available habitat (Harwell and Orth, 2001). However, the relative contribution of dislodged and transported seagrass shoots to the establishment of new seagrass patches remains severely understudied for most species [see also Harwell and Orth (2002)].

While examples of positive influences of fauna like tube worms on the formation of seagrass patches exist, there is also evidence that fauna may negatively modify seagrass structure at the landscape level. Townsend and Fonseca (1998) expanded on earlier work showing that bioturbators can prevent expansion of seagrass beds and studied whether disturbance by stingrays might maintain the existing spatial heterogeneity and patch arrangement of seagrasses (mainly *Z. marina* and *H. wrightii*) in North Carolina, USA. Stingrays were found to disturb sediments to sufficient depth to disturb rhizome elongation, and the return interval of stingray disturbances at one metre resolution was estimated at 1.2 years; thus, stingray disturbance may maintain the spatial structure of these *Z. marina* patches (Townsend and Fonseca, 1998). In a study conducted in Florida, USA, Valentine et al. (1994) reported that large rays could damage *Thalassia testudinum* rhizomes but only at bed edges. In addition, they noted that significant recession of bed edges was recorded as a result of stone crab (*Menippe* spp.) burrowing.

Herbivores of seagrasses such as urchins, turtles, birds, and marine mammals, may also contribute to patch structure (see also Heck and Orth, Chapter 22).

Some recent examples of extensive destruction of wide swaths of seagrass beds by large aggregations of sea urchins have been reported. For example, Rose et al. (1999) documented the removal of 82% of seagrass biomass and >95% of apical meristems along the path of a relatively uncommon urchin aggregation in Florida, USA during a 1-year period. In a Kenyan lagoon, Alcoverro and Mariani (2002) projected the recovery time of seagrasses from urchin disturbance at approximately 99 months, while they estimated the return interval of the disturbance itself at only 44 months, thereby identifying urchin activity as an important structuring agent in selected locations. Dugongs, which feed on both above- and below-ground components of plants, are reported to leave feeding trails and thus enhance edge formation within some seagrass beds, especially those of *Halophila ovalis* (Nakaoka and Aioi, 1999; see also Masini et al., 2001) Lefebrve et al. (1999) also reported that the West Indian manatee, *Trichechus manatus,* fed extensively on patches of *H. wrightii, T. testudinum*, and *Syringodium filiforme* in Florida and Puerto Rico but that even heavily grazed patches recovered from seasonal grazing impacts. Therefore, in some locations and at selected times, herbivore grazing events may remove significant amounts of seagrass and alter the size, shape, and isolation/connectivity of patches.

3. Role of Abiotic Factors

In addition to biotic factors that may contribute to the spatial arrangement of the seagrass landscape, nutrient availability or physical factors such as sediment movement may also play an organizing role (see also Marbà et al., Chapter 6). The patchiness of *C. nodosa* off of northeastern Spain was found to be strongly correlated to the inshore migration of sand waves (Marbà and Duarte, 1995). Robbins and Bell (2000) examined the effect of water depth over a small range (30–100 cm) in mixed patches of *H. wrightii* and *T. testudinum* on a shallow shoal in Florida, USA. Seasonal species-specific depth preferences were noted, but hydrodynamic factors were suggested as potentially more important for seagrass distribution than depth preferences alone (Robbins and Bell, 2000). The effects of nutrient availability at the landscape scale are less straightforward. Nutrient availability was found to be unrelated to the patch dynamics of *Z. marina* in a fjord in the Baltic Sea (Worm and Reusch, 2000). While both slow-release NPK treatments and treatments with live mussels added to plots increased porewater nutrient levels, neither treatment showed consistent results in terms of seagrass shoot growth or shoot addition (Worm and Reusch, 2000).

The idea that physical energy may mold the large-scale patterns of vegetation structure within seagrass landscapes has been suggested with regard to both gap and patch formation. For example, Patriquin (1975) and Wanless (1981) discussed the appearance of "blowouts" in tropical seagrass systems occurring with intense wave and current energy during periods of elevated onshore winds associated with cold fronts in the winter and tropical disturbances in the summer. Kirkman and Kirkman (2000) recently reported blowouts in Australian seagrass beds. Strong physical forces on seagrasses may also affect long-term patterns of seagrass patch dynamics by influencing sexual reproduction. Inglis (2000) noted that the formation of persistent seed banks was reduced in seagrass habitats in Australia that experience strong water flow and suggested that large scale patterns of seed distributions may reflect historical patterns of seed production and disturbance.

The influence of the general hydrodynamic regime on the seagrass landscape has been described in detail in a number of recent papers and is further discussed in Section VI, Chapter 8 (Koch et al.). Current speeds, depth, and a relative exposure index (REI) that incorporates wind speed, direction, and fetch were used to describe areas of seagrass coverage off North Carolina, and landscape pattern was found to be strongly correlated with these physical factors (Fonseca and Bell, 1998). This relationship with physical factors led to the development of a predictive model that can be used to simulate the effect of development and restoration on seagrass landscapes (Kelly et al., 2001; Fonseca et al., 2002). Although predictive modeling of seagrass patch dynamics is only in its earliest stages of development, a few other attempts have also been made. Kendrick et al. (1999) used aerial photographs to show that coalescence of seagrass patches had occurred over a 20-year period (1972–1993) on Success Bank in Australia. They then developed a model for radial increase of patches based on published rhizome elongation rates and aerial photographs from 1972 that was moderately successful in predicting the changes that were seen in successive aerial photographs (1982 and 1993). Fonseca et al. (2004) also used spatially explicit models to predict recovery (recolonization) of aboveground

T. testudinum patches and used this to evaluate revegetation of disturbed areas. With the creation and use of hydrodynamic or spatial models on the rise, physical forces appear to be of tremendous importance to seagrass patch dynamics, and descriptive and predictive models will be important null models in future studies of the structure and function of seagrass landscapes.

4. Gap Dynamics

In the terrestrial realm, the importance of gap dynamics is well known for forest and grassland systems, with implications for landscape structure. The application of gap analysis to seagrass landscapes (e.g. Bell et al., 1999) further expanded the use of landscape methodologies to submerged habitats (see also Duarte et al., Chapter 11). If gap formation is intense and persistent, then a spatial mosaic characterized by areas with missing elements can result. Moreover, gap formation may change the amount of edge habitat or connectivity of the landscape. In seagrass systems such gaps may be produced by physical disturbance causing localized blowouts (e.g. Patriquin, 1975) or by bioturbating organisms (e.g. rays or horseshoe crabs), whose sediment processing frequently leaves pits within seagrass areas, especially species with shallow, fragile root/rhizome architecture. Anthropogenic effects such as boat propeller scars may also cause the removal of seagrass within a bed (e.g. Bell et al., 2002). Macroalgal accumulations (mats) within seagrass beds may also produce gaps within a seagrass bed if the mats are substantial in size and persistent (Holmquist, 1992; Nelson and Lee, 2001). In a seagrass system studied by Bell et al. (1997), such gaps were visibly obvious, variable in size, and generally short-lived (<1.5 year) in the presence of the pioneer seagrass species *H. wrightii*. Gap area has also been linked to extreme sedimentation events (Bell et al., 1999), again suggesting that hydrodynamics and storms may play a major role in modifying seagrass landscapes, and that gap dynamics may be an expression of landscape scale physical energy regimes.

B. Landscape Studies of Seagrass Habitat

1. Faunal Interactions

Having established that seagrass plants can be studied at the landscape scale, an additional area of inquiry is whether landscape principles applied to seagrasses provide new insights into plant–animal habitat relationships (see Chapters 20–22, for additional discussions of animal–seagrass relationships). More specifically, how does a landscape perspective apply to the multitude of organisms that seagrass habitats support? Many worthwhile studies (e.g. Attrill et al., 2000; Lee et al., 2001) have discussed the importance of the physical structure of seagrass to fauna, but since these do not explicitly relate to landscape principles they are not included here. There have been numerous studies, however, that have examined how the spatial arrangement of the seagrass landscape affects the fauna living within, on, and above the seagrass vegetation.

Animal behavior within landscapes can be related to concepts of connectivity or the degree to which landscape arrangement facilitates movement between patches. When connectivity is high, patch isolation is low and animals can percolate across the habitat. However, at some point, declining connectivity may result in an inability of organisms to percolate across a landscape (With and Crist, 1995). Exactly how an organism perceives suitable habitat (e.g. seagrass) is a critical aspect of all these discussions.

In a test of the effects of plant arrangement on the recruitment of copepods in New Zealand, Bell and Hicks (1991) placed artificial seagrass units (ASUs) inside, on the edge of, and outside seagrass beds. Significant differences in copepod recruitment to the ASUs were found as a result of border type, and the importance of studying landscape features of the seagrass in conjunction with fauna was emphasized (Bell and Hicks, 1991). Kurdziel and Bell (1992) also used ASUs to demonstrate that meiofaunal copepods could utilize small patches as corridors for dispersal within a landscape. In both these studies the utilization of ASUs, which allow experimenters to control blade density, blade length, and position of patches, has been quite useful for examining responses of small organisms to landscape features. Where patches of seagrass are large and continuous, however, construction of ASUs becomes logistically problematic, thereby rendering them relatively less attractive experimentally.

2. Patchiness and Macrofauna

Studies of macrofauna and seagrass landscapes have provided some of the best information on landscape influence on faunal survival. Irlandi (1994) tested the effect of 'patchiness' (# patches/area) on the survival of the hard clam *Mercenaria mercenaria* in mixed *H. wrightii* and *Z. marina* seagrass in North Carolina, USA. Analysis of clam survival at three different levels of patchiness with the same total seagrass area showed that survivorship was dramatically greater where the seagrass was continuous (Irlandi, 1994). Similarly, Irlandi (1994) showed that siphon nipping (non-lethal predation) was substantially reduced in continuous seagrass relative to equivalent areas of seagrass that were patchy. Using a similar experimental design, Irlandi et al. (1995) also showed a decrease in survival of bay scallops (*Argopecten irradians*) in patchy seagrass when compared to continuous seagrass after several weeks. Thus, differences in life history features have been found for bivalve fauna that utilize seagrass beds with different landscape characteristics.

Irlandi (1996) expanded her earlier work and examined the effect of physical energy regime (high vs. low), as well as patch size, on two different size classes of *Mercenaria mercenaria*. Large clams grew most quickly in medium-sized patches, and overall more quickly in seagrass than in unvegetated sediment, regardless of physical energy; small clams showed no difference in growth between large and small patches, but did grow better within seagrass than without, and better in high vs. low energy seagrass (Irlandi, 1996). However, the exact cause of these variations in bivalve response to landscape features remains in question. Hovel and Lipcius (2001) pointed out that predator preference for patchy seagrass or a decreased ability to locate prey in continuous seagrass might also explain the observed differences in Irlandi's (1996) study. This series of experiments further highlighted the need to incorporate seagrass landscape features in studies of marine fauna and demonstrated the importance of incorporating physical energy into study design.

Studies of fauna and seagrass landscapes have also focused on blue crabs (*Callinectes sapidus*), a dominant member of the nekton in many seagrass beds on the east coast of USA. Using ASUs to standardize shoot density, Hovel and Lipcius (2001) investigated relationships between seagrass patch size and blue crab survival. Survivorship of tethered juvenile blue crabs increased with decreasing patch size, most likely due to the reduced density of cannibalistic adult blue crabs, the primary predator on juveniles (Hovel and Lipcius, 2001). This inverse relationship between patch size and survivorship also varied seasonally, and habitat complexity was suggested to be a key factor for juvenile blue crab survivorship in both small and large patch sizes (Hovel and Lipcius, 2001). Although only pertaining to juvenile survivorship in a short-term tethering experiment, the counterintuitive result, that a small patch may be more valuable than large ones in some cases, is an interesting finding and illustrates that plant–animal interactions may be more complex than previously considered.

3. Complex Interactions

Other examples of the complex nature of seagrass patch utilization by fauna associated with above ground vegetation also exist. Eggleston et al. (1998) used ASUs of different sizes to test for landscape-level variability in the recruitment of three species of grass shrimps and the blue crab (*C. sapidus*) into patches of different sizes. While all three shrimp species and the smallest size class of blue crabs were able to distinguish small-scale patchiness, the results were not only species-specific, but were also affected by body size and density of animals (Eggleston et al., 1998). In an experimental study utilizing ASUs in Australia, Tanner (2003) reported similarly inconsistent effects of patch shape and orientation on the abundance of different mobile epifaunal species. Species-specific responses to seagrass habitat heterogeneity in Thailand have also been reported for mobile epifauna associated with the seagrass, *Enhalus acoroides* (Nakaoka and Toyohara, 2000) and for benthic infauna in *H. ovalis* and *Thalassia hemprichii* beds (Nakaoka, 2001). Total abundance of epifauna on *E. acoroides* was significantly related to seagrass patch size (Nakaoka and Toyohara, 2000) while both patch size and within patch location were important for infauna at a species-specific level (Nakaoka, 2001).

Studies on sediment-dwelling infauna may also be impacted by seagrass landscape structure. Frost et al. (1999) compared the infaunal community of a continuous expanse of seagrass (*Z. marina*) in Britain to that of a fragmented assemblage of adjacent patches. The infaunal communities were found to be significantly different in composition, reflecting a large increase in polychaete abundance in unvegetated areas of the fragmented bed (Frost et al., 1999). The most plausible explanation for these community patterns was a change in grain size of the sediment as landscape features were altered (Frost et al., 1999). On the other hand, Bowden et al. (2001) found that infauna communities in *Z. marina* in England varied with patch size and within-patch location, but concluded that the most likely factor causing the observed differences was small differences in physical parameters. Clearly, then, effects of landscape structure on infauna and epifauna tend to be variable and species-specific, emphasizing the importance of considering landscape parameters in the design of seagrass and subtidal experiments.

4. Mobile Fauna and Patchiness

Large mobile organisms are also common in seagrass ecosystems and recently studies have begun to examine their abundance and movement with reference to seagrass patch structure. MacArthur and Hyndes (2001) reported that fish (Family: Odacidae) community composition varied with degree of seagrass patchiness, although the seagrass species composition also varied with patch density. Salita (2000) examined fish abundances in the Philippines and determined that the first two components of a Principal Components Analysis [‘continuity of vegetation’ (including patch size and number) and fractal dimension] explained 77% of the variation in fish abundance measured [see also Salita et al. (2003)]. In an examination of intertidal and subtidal landscape mosaics composed of seagrass, mangroves, and unvegetated sediments, Pittman (2002) found evidence that species of fish and prawns had variable responses to the reduction of seagrass within these mosaics. However, he did note that below a cover of 15–20%, most seagrass patches in fragmented areas ceased to support seagrass-associated fish. Thus, information is starting to emerge to suggest that large nekton can also respond to landscape-scale features of the seagrass habitat mosaic.

Seagrass beds have most commonly been studied at the single patch scale or in landscapes made up of a single patch type, but some studies have adopted a broader view by investigating landscape mosaics composed of multiple patch types (see Fig. 2). By illustrating that nekton displayed a strong preference for benthic mosaics that contained an abundance of seagrass patches, Pittman (2002) reinforced and extended the importance of seagrasses in benthic landscapes. Moreover, Irlandi and Crawford (1997) reported that adjacency of seagrass habitat influenced faunal abundance in salt marshes. Specifically, pinfish (*Lagodon rhomboides*) were substantially more abundant in salt marshes located adjacent to seagrass beds than in marshes spatially distant from seagrass beds. The authors suggested that pinfish movement could be a mechanism for transfer of secondary production between marsh and seagrass, and argued that consideration be given to preserving and restoring such closely linked systems as a composite rather than either habitat alone (Irlandi and Crawford, 1997; see also Bell et al., 1997). Finally, Micheli and Peterson (1999) suggested that seagrass beds may act as corridors for the movement of predatory blue crabs between large oyster reefs and smaller, separate reefs, postulating that fragmentation of the intervening seagrass beds could alter the community composition of benthic macroinvertebrates on oyster reefs.

5. Multiple Spatial Scales and the Landscape Approach

A uniquely ‘landscape ecology’ methodology is to conduct investigations over multiple spatial scales. Turner et al. (1999) examined infauna in seagrass sites dominated by *Z. novazelandica* in New Zealand at both the patch and the landscape scale, finding that the landscape level analysis explained significantly more of the variation in faunal abundance than the patch scale analysis. Notably, the authors suggested that a landscape metric, fractal dimension (D) of the habitat, was a primary factor underlying the variation in infaunal abundance. Further, landscape level effects on abundance were not necessarily related to effects observed at a smaller scale (Turner et al., 1999). In another multi-scale study Bell et al. (1995) illustrated that, for some ecological processes, seagrass beds cannot be treated as larger versions of seagrass patches. In an experiment with ASUs of different sizes, large (4 m^2) patches collected disproportionately greater amounts of drift algae than small (1 m^2) patches. These studies suggest that it may be inappropriate to infer large scale features of seagrass landscapes from measurements made at small, local scales (*sensu* Fonseca et al., 2000).

Finally, the landscape scale may not be the largest scale of interest in all cases. A recent study by Hovel et al. (2002) highlights the complex nature of the relationship between seagrass landscape structure and fauna in a North Carolina, USA system. They found that landscape features (% cover and total linear edge of beds) could explain little of the local patterns of abundance of fish and epibenthic crustaceans. Instead they suggested that processes operating beyond the landscape (e.g. proximity to inlets, larval delivery) might need to be considered (Hovel et al., 2002). Similar ideas were proposed by Bell et al. (1988) based upon studies of seagrass, decapods, and juvenile fish. Bell and Hall (1997) also reported that spatial location within an estuary best explained patterns of macroalgal accumulation in seagrass beds in Florida, USA. These studies suggest that some ecological attributes may reflect processes that operate over spatial scales that exceed the dimensions of a local landscape.

IV. Terrestrial vs. Marine Landscapes

Researchers have come to recognize that the landscape approach commonly applied to terrestrial studies may be useful in marine studies. However, a number of findings from the seagrass landscape studies discussed above reveal marked differences in factors controlling seagrass vs. terrestrial landscapes. Notably, seagrass landscapes, although also formed by angiosperms, appear to be dynamic on a far shorter temporal scale than the forests that are often a focus of terrestrial landscape studies, making it critical that a sampling regimen be adequately replicated in the short-term. Robbins and Bell (2000) also suggested that many of the responses to disturbance typically recorded in terrestrial systems (e.g. succession) may not be common in at least some seagrass ecosystems, highlighting further the interesting divergence in some aspects of offshore vs. onshore landscapes.

Dissimilarities between terrestrial and subtidal landscapes may be a result of limited seed production by seagrasses and/or the highly monospecific character of the seagrass beds in the some of the areas studied. In contrast to terrestrial systems, where gaps serve as sites for seed recruitment and offer areas for invasion by additional plant species (e.g. Grubb, 1977), Bell et al. (1999) found that gaps within monospecific seagrass beds in Tampa Bay, Florida were not invaded by other species (see also Robbins and Bell, 2000; but see Williams, 1990). Additionally, the limited studies available on disturbance gaps and boat propeller scarring within seagrass beds show little evidence that gaps expand and propagate in these systems (Dawes et al., 1997; Kirkman and Kirkman, 2000; Bell et al., 2002; but see Whitfield et al., 2002), resulting in the familiar wave regeneration patterns often seen in forests. In contrast, subtidal marine landscapes are more likely to be regularly disturbed than many terrestrial settings due to the increased kinetic energy of the fluid medium in which they grow, resulting in short return intervals of disturbances. A final difference is that much of the change in cover in seagrass landscapes (e.g. gap closure) in many areas purportedly occurs via growth of rhizomes belowground (Robbins and Bell, 2000; Jensen and Bell, 2001), rather than by the closing of the canopy or by germinating seedlings. Thus, some of the basic ideas pertaining to disturbance and habitat heterogeneity (particularly with respect to recruitment and spread of disturbance—e.g. percolation), which appear to work adequately for terrestrial systems like forests and arid grasslands, do not appear to be as straightforward in subtidal landscapes.

High levels of disturbance lead to fragmentation, and impacts of seagrass habitat fragmentation on fauna, resulting in a decrease in connectivity and an increase in patch number, appear also to differ from those that have been reported for fauna from terrestrial systems. A major distinction is that spacing between underwater seagrass patches, in contrast to patch spacing in terrestrial landscapes, may often be insufficient to hinder dispersal of organisms between patches given the important role of passive transport with water currents in the dispersal of marine organisms (Sogard and Able, 1994; Bell et al., 2001). Conceivably, some of the impacts of fragmentation on fauna may only be observed at a greater degree of patch isolation than that typically examined in past studies or in terrestrial landscapes, or when patches are sufficiently large that edge and core areas are functionally established. However, little information exists presently on resource availability or predator distribution for fauna found at edges of seagrass beds (e.g. Bologna and Heck, 2002; also see below). Findings on seagrass bed fragmentation by propeller scarring, combined with other studies on faunal response to seagrass plantings (e.g. Fonseca et al., 1996) or faunal abundance in seagrass patches of different sizes (McNeill and Fairweather, 1993) seemingly agree that many of the dominant epibenthic fauna in seagrass beds do not appear to be limited by the amount of seagrass cover/density, at least over the scale at which many studies have been conducted and at the degree of fragmentation examined (see also Attrill et al., 2000; Hovel et al., 2001; Uhrin and Holmquist, 2003). It is important to note, however, that logistical considerations have often limited experimental studies investigating relationships between seagrass patch size and fragmentation vs. faunal abundance to utilizing experimental units (such as ASUs) which, while feasible to manipulate and replicate, may be of limited use because of their small size. Therefore, our ability to evaluate the impacts of fragmentation via experimentation is restricted to small extents at this time.

V. Landscape Dynamics

A. Disturbance and Growth

Studies on seagrasses have documented that seagrass distribution is strongly related to physiological tolerances and other growth restrictions including water depth, light attenuation, and salinity zonation (see Marbà et al., Chapter 6; Zimmerman, Chapter 13). Superimposed upon this autecological template are biotic factors such as grazing or competitive interactions, which may contribute to the observed spatial arrangement of seagrasses. One of the challenges emerging from past studies of seagrass landscapes is to determine how disturbance may act synergistically with such abiotic or biotic factors to produce changes in landscape features.

Disturbance is a major factor determining spatial heterogeneity of landscapes (Baker, 1992) often changing the substrate, the physical environmental, and resource availability (Farina, 1998). Disturbance has a number of attributes including frequency, intensity, and size (see White and Pickett, 1985) that are all related to the extent of landscape modification. While disturbance is known to shape and change seagrass landscapes, few studies have examined the influence of disturbance on the physiognomy of landscapes dominated by clonal seagrasses (but see Marbà and Duarte, 1995; Bell et al., 1999). Physical disturbance, whether biological (Townsend and Fonseca, 1998) and/or physical (tidal currents, waves, sedimentation; Fonseca and Bell, 1998; Fonseca et al., 1998; Robbins et al., 2001; Koch et al., Chapter 8), may shape the spatial patterns of seagrass landscapes by causing gaps within seagrass beds (Bell et al., 1999), and/or by influencing the lateral growth behavior of the seagrass itself (Marbà and Duarte, 1995, Townsend and Fonseca, 1998; Fonseca et al., 2002). Disturbance on seagrass landscapes may even leave a spatial signature if seagrasses cannot quickly reoccupy the disturbed area of a seagrass bed (as many species cannot), providing an opportunity to follow temporal sequences of landscape development.

Regrowth of seagrass patch margins has been directly measured (e.g. Jensen and Bell, 2001) and closure of gaps (especially those <10 m^2) is common within at least one seagrass landscape (Bell et al., 1999). With both margins and gaps, closure can occur via vegetative growth or seedling recruitment. Some seagrass species (e.g. *Z. marina*) have an abundant seed supply and are capable of repopulating gaps via seeds and/or reproductive shoots (e.g. Orth et al., 1994; Inglis, 2000). Other species often have reduced flowering and, consequently, belowground growth patterns rather than seedling recruitment play a major role in gap closure, regardless of the disturbance mechanism (see Rasheed, 1999; Bell et al., 1999). Gap closure rate via belowground growth varies among species with rhizome elongation rates being highly variable both across (e.g. Hemminga and Duarte, 2000) and within species (e.g. Jensen and Bell, 2001). A third mechanism of gap closure may be regrowth of short shoots from buried rhizomes. Gap closure could occur if sediments shift sufficiently to allow regrowth from previously buried belowground components, or if shoots are able to elongate vertically at a sufficient rate to outpace sedimentation (Marbà et al., 1994). However, the capacity of some seagrasses to persist after burial may be limited (Mills and Fonseca, 2003).

B. Pathogens and Disease

Disease, another example of disturbance in seagrasses, is itself influenced by a host of factors. Seagrass disease may cause impacts to the landscape on a par with more commonly measured disturbances (Entel and Hamilton, 1999). When a major component of the landscape is infected by a pathogen then (as is often true for other forms of disturbance) the potential exists for loss of that component from the landscape, leading to gap formation and/or fragmentation of the habitat. Some marine communities (corals) have been reported to be less likely to recover from disease than from severe physical disturbances such as hurricanes (e.g. Bythell et al., 2000) but whether this applies at the landscape level remains untested for seagrasses.

In seagrass systems, the pathogenic stage of infection by protists of the genus *Labyrinthula* causes lesions easily visible as dark longitudinal bands on seagrass blades (Muehlstein et al., 1991; Burdick et al., 1993). In some cases *Labyrinthula* spp. does not cause noticeable harm to the seagrass host (Vergeer and den Hartog, 1994). But in some locations disease incidence may be high and lesion cover extensive (Burdick et al., 1993). Ralph and Short (2002) recently provided convincing data that *Labyrinthula* spp. is a primary pathogen of *Z. marina* and that infection by this saprophytic 'slime mold' (*sensu* Muehlstein et al., 1988) may operate as a modifier of landscapes by increasing the mortality rate of seagrass shoots or ramets and reducing the overall photosynthetic capacity of the seagrass plant (see also Moore and Short, Chapter 16).

Seagrass die-offs in the past have been linked to outbreaks of *Labyrinthula* spp. Infection of the temperate seagrass *Z. marina* by *Labyrinthula zosterae* is thought to have caused the 1930s 'wasting disease' that dramatically reduced seagrass cover in the entire North Atlantic (DeJonge and DeJonge 1992; Duarte et al., Chapter 11) and is suspected to be a primary cause in the decline of some seagrass patches more recently (Short et al., 1986; Short et al., 1988; Burdick et al., 1993). Occasionally, complete local landscapes may be lost and/or replaced with new structural elements (e.g. loss of *Z. marina* in the northeastern USA and its replacement by macroalgae; Short et al., 1988). Studies comparing the temporal spread of infection with rates of change in spatial patterns, along with information on environmental conditions (physical parameters), may help identify what factors (e.g. salinity, temperature) might be associated with highly contagious events of extensive lesion cover. A crucial challenge is to be able to identify under what conditions outbreaks of disease may (and do) occur in seagrass systems, and to link such changes to changes in the landscape mosaic.

C. Algal Blooms and Macroalgae

Algal blooms, including invasions by some rhizophytic macroalgae of the genus *Caulerpa,* may also alter seagrass landscape structure. Such blooms have become common events in selected geographic locations. For example, *Caulerpa taxifolia* was recently introduced into new areas of the Mediterranean where it has established both persistent and expanding populations (Meinesz and Hesse, 1991; Kenworthy et al., Chapter 25). This rapidly growing species can spread across long distances by fragmentation and may outcompete other vegetation in the shallow water habitats. *Caulerpa taxifolia* is thought to be competitively successful because it (1) extends laterally across the substrate as well as branching upward into a large, dense mat without requiring a solid structure for attachment, and (2) it can survive and thrive in the low light conditions present in the subcanopy of other vegetation (Boudouresque, 1997). *Caulerpa* species also contain large amounts of secondary metabolites and are highly unpalatable to most herbivores (Lemee et al., 1996), thereby reducing the potential for control by grazing. Secondary metabolites may also severely limit epiphyte attachment. In combination, reduced herbivory and epiphyte load may facilitate growth and fragmentation of *Caulerpa*, and thus increase landscape coverage.

Detailed impacts on seagrass systems caused by the increasing dominance of *Caulerpa* species are starting to be recognized, especially in European waters. For example, researchers have reported that *C. racemosa* can displace seagrass by overgrowing seagrass blades as well as invade bare areas more quickly than seagrass (Ceccherelli et al., 2000). Close examination of *Caulerpa* in seagrass beds has revealed that these macroalga can overgrow rhizomes of seagrasses (De Villele and Verlaque, 1995). Additionally, *C. taxifolia* has been reported to cause chlorosis and decreased abundance and longevity of *Posidonia oceanica*, and invasion of seagrass beds has also been followed by deterioration of rhizomes and roots with a corresponding increase of hypoxia in sediments (De Villele and Verlaque, 1995). The appearance of invasive *C. taxifolia* on the west coast of the USA has recently sounded an alarm call as well. However, rapid and extreme efforts to eradicate *C. taxifolia* upon arrival have thus far prevented the predicted smothering of California coastal ecosystems predicted by Jousson et al. (2000). Assessments of the large scale dynamics in the spatial structure of a seagrass ecosystem when influenced by macroalgal blooms would be most effective using a landscape approach.

Further interaction of seagrasses and macroalgae has been seen in the creation of gaps linked to macroalgal accumulation disturbances, which may lead to increased heterogeneity of faunal components within seagrass landscapes. Using an experimental approach, Holmquist (1997) created gaps in seagrass (mostly *T. testudinum*) in Florida, USA by inserting macroalgal clumps into seagrass areas. These experimental plots showed increased abundance and evenness of mobile canopy fauna in comparison to unaltered seagrass control plots after 6 months, although the transitory nature of the drift algae probably made this a temporary effect overall (Holmquist, 1997). The interaction of macroalgae and seagrass landscapes may be even more complex, since faunal colonization of new seagrass patches was found to be facilitated in Florida, USA by drift algae (Brooks and Bell, 2001), the very same agent of disturbance to established beds in the seagrass landscape studied by Holmquist (1997).

Large-scale disturbance events such as storms or hurricanes may also have major impacts on seagrass spatial structure, but few data have been specifically collected to support this suggestion. Fonseca et al. (2002) reported that disturbance from intense storms was linked to landscape change of seagrasses in North Carolina, USA. A decrease in patch size was detected due to edge erosion during storms in $50 \times 50\ m^2$ study areas (Fonseca et al., 2002). However, landscape alteration varied with patch size and physical exposure; greater overall decreases in patch size were found in higher energy areas (small patches present) than in less exposed areas (larger patch sizes) (Fonseca et al., 2002). These findings again illustrate the interaction between landscape structure and disturbance. Recent models developed by Fonseca et al. (2002) and discussed by Fonseca and Bell (1998) provide one methodology for measuring the physical setting of seagrass beds linked to extreme events and then predicting landscape structure.

VI. Boundaries and Seagrass Landscapes

Within landscapes, boundaries represent zones between two contrasting patches, which delimit heterogeneity (Cadenasso et al., 2003). In terrestrial applications of landscape principles, boundaries or edges represent areas of special function (ecotones). The consistency with which the special functions seen in terrestrial ecotones apply to seagrass landscape boundaries is not yet clear, but is of particular interest because boundary zones may make up a significant portion of benthic landscapes (Zajac et al., 2000). Seagrass beds that have a large number of patches may have substantial amounts of edge. In seagrass systems, simple boundaries are typically many easy to observe visually due to the sharp contrast between dense seagrass vegetation and the unvegetated sediment matrix (e.g. Kendrick et al., 1999; see also Fig. 1). However, more complex landscapes with overlapping patches resulting in mixed boundary regions are common, and whether these mixed areas function as ecotones or should be treated as independent patch types is not clear at this time. Therefore more work delineating boundary properties in seagrass landscapes would be particularly useful.

Some new approaches to the study of ecotones in general have recently been proposed. Strayer et al. (2003) devised a general functional classification scheme for boundaries that appears useful for seagrass systems. Specifically, they classified boundaries as reflective, transforming, absorptive or semipermeable with respect to fluxes of materials across patch edges. Accordingly, the fate of nutrients, wave energy or sediment particles across seagrass patch boundaries could be studied in this context. A similar approach of following material movement across ecotones could be used to follow how populations of plant or animal taxa are influenced by passage across seagrass patch boundaries. For example, Brooks and Bell (2001) found that amphipod dispersal from drift macroalgae was reduced after passing from the interior of a seagrass bed through the seagrass/sediment boundary, suggesting that for at least some small mesograzers, such boundaries are readily perceived and act to modify dispersal rates. Determining the functional nature of seagrass patch boundaries will be an important step in understanding the implications of landscape changes (e.g. increasing fragmentation) that increase the proportion of habitat edges.

Much of the existing information on seagrass edges focuses on faunal usage of edge vs. interior of seagrass beds. To date no consistent spatial patterns of faunal habitat utilization have emerged. Bologna and Heck (2002) found little consistent support for differential use of seagrass bed edges (defined by authors as the outer 1 m of a bed) by macrofauna compared to interior regions of beds, although secondary production of some peracarid crustaceans was significantly higher in interior areas of seagrass beds compared to edges. Similarly, Sanchez-Jerez et al. (1999) found that macroepifaunal abundance did not differ between edges and interior of seagrass beds. Other studies have found that some faunal taxa are more abundant at edges of beds (scallops; Bologna and Heck, 1999; mysids; Barbera-Cebrián

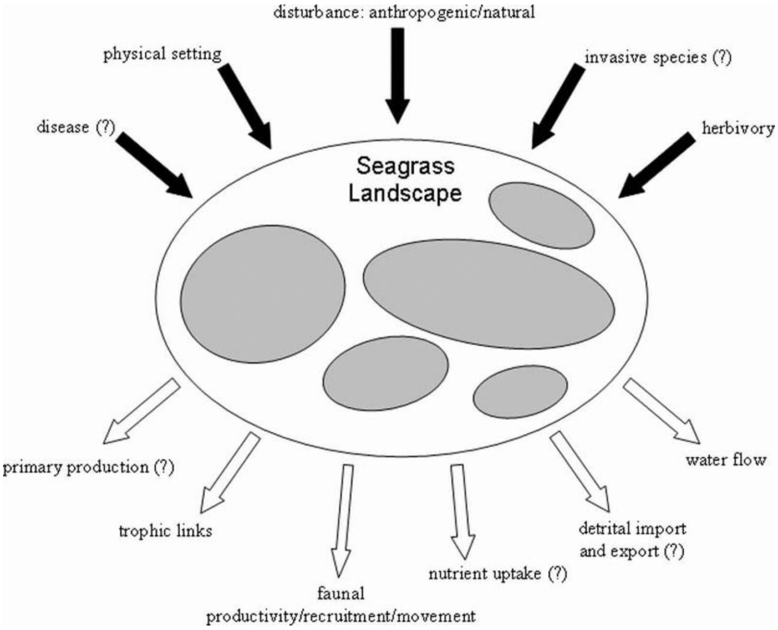

Fig. 4. Summary of major biotic and abiotic factors suggested to modify seagrass landscapes (filled arrows); ecosystem structure and functions modified by landscape characteristics (open arrows) are also shown. (?) indicates poorly known at this time.

et al., 2002; shrimp; Rizzuto, 2003). Understanding of how edges of seagrass beds modify population, community or ecosystem level features of faunal assemblages is poor at this time, and this is an area worthy of further exploration. As discussed by Fortin et al. (2003), it is critical to consider how one defines the extent of patch edges given that this definition must be driven by the perceptual scale of the organism of interest.

VII. Conceptual and Methodological Improvements

Our understanding of factors modifying seagrass landscapes and implications of seagrass landscape structure for ecosystem function has developed conceptually over the last 15 years (Fig. 4). However, while interest in the study of seagrass landscape ecology has increased recently, numerous limitations remain to the application of terrestrial landscape techniques to the subtidal landscape. Perhaps one of the most pressing problems revolves around the generation of adequate spatial representations of seagrass landscapes. Fortunately, with advances in remote sensing capabilities (see Dekker et al., Chapter 15) and the increasing use of Geographical Information Systems (GIS) for analyses, seagrass spatial data at the landscape scale should become more accessible to researchers over time, and our ability to develop spatially explicit landscape models should consistently improve, providing better tools to management and improving the success of restoration projects (Bell et al., 1997; Kelly et al., 2001; Dekker et al., Chapter 15).

As the use of a landscape approach increases in seagrass systems, so too must the documentation of the uncertainty or limitations in the data used to construct model landscapes. Major categories of uncertainty of spatial data include positional accuracy, correct categorization of attributes and attribute consistency, data resolution, and user interpretation of data. Edwards and Fortin (2001) argue that the degree of uncertainty in detecting landscape pattern is related to sampling design and spatial resolution of data, as well as patterns of metric sensitivity (see also Hargis et al., 1998). The overriding benefit of providing information on uncertainty is to be able to convey to other researchers the fitness of a data set for an intended application. A comprehensive treatment of the issue of uncertainty of spatial data is provided in Hunsaker et al. (2001).

An important emphasis must also be placed on the collection of appropriate and sufficient data to conduct landscape analyses. For example, software programs will readily perform spatial interpolation of vegetation cover from even a few, widely dispersed data points, but the interpretation of the output cover surface must take into account that the information is very likely highly inaccurate (especially for patchy cover types). Kriging and other forms of geostatistical analysis provide reportable error estimates by taking spatial autocorrelation of data into account, making their application highly desirable for spatial analyses. This becomes especially important when spatial representations are being compared and/or become the basis for management decisions.

Lastly, given the many issues related to scale as noted in the literature, how can and should such considerations be applied to seagrass landscape ecology? For example, a recent paper by Balestri et al. (2003) reported that both large (10 km) scale and very small (1 m) scale variation in morphology and growth of *Posidonia oceanica* was recorded, illustrating that some environmental factors may have impacts over multiple scales. There are few seagrass studies that specifically utilize geostatistics (Fonseca, 1996) or that directly assess scale issues (Bell et al., 1995; Fonseca et al., 2002). Otherwise, the problem of non-independence between seemingly independent samples due to spatially coherent variability (spatial autocorrelation) has been most directly addressed in mensurative ecological studies, such as those using GIS. As a general rule, some knowledge of the spatial scale of environmental variation in abiotic and biotic factors (e.g. sediment composition, plant density, and composition, currents, temperature, etc.) within the landscape extent at a given sampling resolution must be established, and adjustment of sampling effort made accordingly. Moreover, relying on randomization or lattice designs to account for systematic trends in variation also stands little chance of detecting anisotropic (direction-dependent) sources of measurement error (Fonseca, 1996). Thus, orientation of the experimental layout may also carry embedded sources of bias, which need to be considered in the design and analysis of landscape level studies.

VIII. Future Directions

A number of topics emerge from our review above as logical topics worthy of future investigation. From a plant perspective, the study of seagrass population biology in a spatial context remains a critical need. Information on how growth patterns of rhizomes and patterns of seed recruitment contribute to the spatial heterogeneity of seagrass landscapes is sorely lacking. Data from restoration studies or recovery of propeller-scarred seagrass areas may provide some unique insight into these topics.

From a landscape perspective, an explanation of the mechanisms of patch origin and the processes that control their shape and arrangement would be a major advancement. Within seagrass landscapes, information on both biotic and abiotic factors that affect the maintenance of boundaries would improve our understanding of mechanisms responsible for changes in landscape structure over time and space. For example, are the edges of patches highly influenced by bioturbation and is this consistent over the landscape? Are patch boundaries resilient to extreme storm events and does resiliency vary among patches of different sizes of different species? How much change occurs at edges vs. interior gap areas of seagrass patches? Are changes in patch boundaries accompanied by variation in faunal activity or movements? These questions, building upon results from previous investigations, incorporate a new focus on edges of patches and are logical extensions to studies of patch dynamics (see also Duarte et al., Chapter 11).

Faunal relationships with seagrass landscape features are often inferred from sampling regimes that provide limited data on behavior of organisms within patches of different characteristics, due in part to a fluid medium that imposes limits on visibility. Similarly, quantitative information on movement patterns of fauna throughout landscapes is also sorely lacking. Much of the excellent data on fauna–landscape associations in terrestrial systems has emerged from visual observations of animal use of habitat (e.g. nesting sites) and by tracking of movements. Techniques to acquire such information in seagrass landscapes are a necessity if we are to improve our interpretive power concerning faunal–landscape relationships. Video camera systems that capture detailed records of animal activities may serve as one potential source of behavioral information to evaluate landscape percolation and connectivity. Acoustic telemetry may also be a useful tool for tracking animal movement in seagrass landscapes.

Recently, Wu and Hobbs (2002) argued that while much attention in landscape ecology has been directed at describing spatial patterns, more emphasis needs to be aimed at understanding how landscape patterns affect flows of materials (energy, materials, organisms, information) across the landscapes. Likewise, for landscape ecology to improve, a better ecological understanding of the relationships between the metrics used to quantify spatial structure and ecological processes must evolve. The above recommendations are certainly also true for seagrass systems. Currently, deciphering which metrics allow the best characterization of seagrass landscapes remains a relatively unexplored and important challenge.

IX. Summary

In summary, although only recently applied to seagrass landscapes, the principles of landscape ecology have already yielded much new information about the growth patterns of seagrasses and their ability to recover from disturbance (natural and anthropogenic), as well as providing a new, ecologically relevant framework from which to examine the dynamics of faunal populations within the seagrass habitat (e.g. Fig. 4). Landscape studies of seagrasses have advanced from initial efforts at describing patch dynamics to the beginnings of predictive modeling. Examining faunal communities in the context of the seagrass landscape has revealed the complexity of interactions between organism and habitat. Both plant and animal studies applying a landscape approach in seagrass settings have revealed noteworthy departures from terrestrial paradigms. Future studies will likely result in new and interesting discoveries and a better understanding of subtidal marine landscapes as a whole.

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Epilogue

This book has been the outcome of four years of intensive preparation and, as pointed out in the "Foreword" is based on three decades of intensive research into seagrasses. However, having assembled a group of the finest seagrass biologists in the world who have produced a magnificent set of 26 chapters, encompassing most areas of seagrass biology, the editors do not think that we have reached any kind of final statement of seagrass research. Much as we hope that this book will provide stimulus and ideas for generations of seagrass workers to come, we see this book merely as a guidepost early on the road to an understanding of the role of seagrasses in coastal ecosystems and to the proper conservation of these important species. In closing this book we would therefore like to add what we think are a few pointers to the future.

In reviewing seagrass research we need to assess our strengths and our shortcomings. The strengths are clearly embedded in the record of the 26 chapters of this book and we should not forget the dedication of a vast body of workers who have contributed to this corpus of knowledge. Nevertheless we should face the future with a clear vision and recognize a number of shortcomings in the past. Some of these are methodological – past techniques were not sufficient for the purpose. Some were based on paradigms which we no longer support – such as the ascendancy of primary production by the seagrasses of seagrass beds as opposed to that of the epiphytes and benthic algae (Chapter 7) or the role of predators in structuring seagrass beds (Chapter 22). Undoubtedly new paradigms will emerge in the future and we should make sure that we retain the mental flexibility to be receptive to these. We should also bear in mind the balance between the need to produce adequate frameworks for synthesis and comparative analyses of seagrass ecology and the realization that not all seagrasses are the same and that the same species of seagrass may not perform the same role at the different sites at which it occurs around the world. Neither will of all them fit into the neat categories that we try to fit them into. Large canopy-forming seagrasses will clearly differ in many ways from *Halophila* species and other smaller seagrasses.

There is also a pressing need to find ways to integrate seagrass research, not only in terms of seagrass disciplines (taxonomy, population genetics, physiology, ecology, conservation, etc.) but also in terms of the wider disciplines of integrative ecosystem conservation and management at the local, community, the regional area and the global level. In the past seagrass researchers have been satisfied to address specific biological and conservation topics. In the future it will become increasingly important to integrate this knowledge into two other activities, i) addressing what the community wants in terms of land use of seagrass areas and ii) best management strategy for any given area, in terms of local and global imperatives. This is a challenging area but there has been much progress made here, in terms of fostering community interest in seagrasses (e.g. SeagrassNet, Seagrass Watch, etc) and in getting governments and NGOs interested in seagrass value and conservation.

In order for conservation efforts to meet the broadest possible support it is important to present the many important roles and the general value of seagrasses in an effective way. In the Foreword to this book we listed a number of those values. However that list is by no means exhaustive and local communities or global organizations may see other priorities and values to seagrasses. For example seagrasses have cultural importance locally to many indigenous communities around the world and they may form a significant part of their economy.

In the broader, global context seagrasses have an important value as bioindicators. They are widespread, being present on all continents except Antarctica, and several species have a very wide range, e.g. *Halophila decipiens* and *Zostera marina*. Others form a significant component of the ecosystem in many areas, sometimes being the dominant organisms defining the ecosystem e.g. *Zostera, Thalassia* and *Posidonia* beds. As such they are responsive to perturbations to the environment and are importantly integrative of many environmental conditions. Thus seagrasses have been used in a number of important wide-scale and multidisciplinary studies such as the Florida Bay study (Chapter 23), the Chesapeake Bay studies (Chapter 25; see also references), the Moreton Bay study (see “References”) and the Cockburn Sound study (see Chapter 23).

In the future it will be important for seagrass biologists to canvas these special qualities of seagrasses and seek ways of bringing seagrasses to the forefront. This can be done by recommending the use of seagrasses in all future interdisciplinary investigations of the nearshore environmnent, by incorporating such a viewpoint into national and international legislation, where appropriate, by ensuring that seagrass biologists are always an integral part of multidisciplinary investigations of the nearshore environment, by promoting special sessions of national and international conferences, by supporting existing journals devoted to seagrass research and stimulating new journals, and in many other ways.

We hope that the contents of this book provide a useful departure point to face the future challenges in seagrasss research and conservation. Although the editors and authors have made all possible efforts to ensure that the contents of the book represent the most updated depiction of current knowledge as possible, we sincerely hope that they soon become outdated. This would be the best possible symptom of the major progress in understanding the biology, ecology and conservation of seagrasses this book strived to stimulate.

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Seagrass Watch: Email, Seagrass@dpi.qld.gov.au

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