Near-Coastal Seagrass Ecosystems

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Contents

Abstract

- Seagrasses are the only marine-submerged angiosperms, and there exist approximately 60 species of seagrasses, worldwide.
- Tropical and temperate seagrass ecosystems are markedly different. Temperate seagrasses are larger and beds are denser. Temperate seagrasses respond to seasons and water temperature whereas tropical seagrasses, although also responding to seasons, i.e., wet and dry, do not show growth correlations with changes in water temperature.
- Globally many seagrass beds have been lost, and many more are threatened by human activities; protection is vital. Reduced light (due to eutrophication of coastal regions and sediment disturbance) is the single most important cause of seagrass loss.

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- Seagrass beds support numerous invertebrates and juvenile commercially and recreationally important fish and crustaceans. Many of these dependent animal communities are herbivorous but few eat seagrasses. Plants and animals growing on seagrass lead to complex food-web communities, with numerous trophic levels. Many birds and mammals use seagrass ecosystems as sources of food, despite using other coastal ecosystems for habitation.
- Seagrass beds are a sink for nutrients delivered from terrestrial runoff and detritus from seagrass beds and other marine ecosystems. These nutrients support their extensive food web. Seagrass beds are also a significant net sink for atmospheric carbon storage.

Introduction

Restoration and remediation of seagrass ecosystems have not met with great success. The use of vegetative propagules as a means for reestablishment of seagrass beds has been plagued with difficulties due to mismatches between propagule sources and targeted restoration beds. Removing vegetative propagules from donor beds leads to problems of the donor beds recovering. Growing seagrass from seed is not always a viable option for restoration because of the vulnerability of seedlings and poor recruitment into unvegetated areas. Remediation of destroyed seagrass is not often successful. An understanding of levels of genetic diversity and spatial genetic structure can contribute to improved restoration outcomes by identifying the most genetically appropriate source material for restoration sites. The discoveries made recently through DNA analysis and phylogenetic affinities have also helped untangle some of the taxonomic identities of seagrass and led to better decisions as to the choice of restoration sources and materials.

The ancestors of the higher plants left the sea some 400 million years ago, but the seagrasses are the only ones to have returned to a completely submerged marine existence. This polyphyletic group of flowering plants reinvaded the sea probably about 100 million years ago in the Cretaceous (Larkum and den Hartog 1989). Our current knowledge of species affinities and phylogenetic origins is poor for this group of plants and requires urgent improvement in order to better inform management and researchers (Table 1). A stable taxonomy is a necessary base for all botanical research. Morphological and anatomical variations within the species are not systematically documented, and it is recommended that samples of material used for molecular, physiological, and morphological research are deposited in recognized herbaria.

There are about 60 species of seagrass in the world in 13 genera (Table 1). *Ruppia* and *Lepilaena* are often grouped among the seagrasses but can grow in brackish and fresh water. There are so few seagrass species globally and locally, and a large degree of endemism that the loss of one species may mean thousands of other organisms are lost. Kuo and den Hartog (2001) describe all seagrass to that date and offer a key for their identification.

Table 1 List of seagrass species of the world. The distributions have been taken from Green and Short (2003). The Seagrasses of the World. There is still taxonomic activity deciding on whether some species here are real species or strains of others. Distributions too are unclear in some cases

Family	Genus	Species	Distribution
Zosteraceae	*Zostera*	*marina*	Europe, North America
		caespitose	Japan
		caulescens	North Korea and Japan
		asiatica	Korea and Japan
		noltii	East Atlantic, Baltic, Mediterranean, Black, Caspian, and Aral Seas
		japonica	Japan
		capensis	Southern Africa
		capricornii	Australia
		muelleri	Australia
		mucronata	Australia
		novazelandica	New Zealand
	Phyllospadix	*scouleri*	Western North America
		torreyi	Western North America
		serrulatus	Northwestern North America
		iwatensis	Korea, China, and Japan
		japonicus	Korea and Japan
	Heterozostera	*tasmanica*	Southern Australia
		polychlamis	Southern Australia
		nigricaulis	Southern Australia
		chiliensis	Chile
Cymodoceaceae	*Halodule*	*uninervis*	Tropical and subtropical Australia, West Africa, SE Asia, India, Pacific
		beaudetti	Northeast Madagascar, Caribbean
		wrightii	Global
		bermudensis	Bermuda
		ciliate	Tobago Island, Panama
		pinifolia	Indo-West Pacific
		emarginata	Brazil
			Mediterranean and North Africa
			Indo-West Pacific
	Cymodocea	*nodosa*	Indo-West Pacific
		rotundata	Northwestern Australia
		serrulata	Caribbean, Florida
		angustata	Indo-West Pacific
	Syringodium	*filiforme*	Indo-West Pacific
		isoetifolium	South Western Australia
	Thalassodendron	*ciliatum*	Southern Australia
		pachyrhizum	Southern Australia
	Amphibolis	*antarctica*	Southern Australia
		griffithii	South western Australia

(*continued*)

Table 1 (continued)

Family	Genus	Species	Distribution
Posidoniaceae	*Posidonia*	*oceanica*	Mediterranean
		australis	Southern Australia
		sinuosa	Southern Australia
		angustifolia	Southern Australia
		ostenfeldii	Southern Australia
		robertsoniae	Southern Australia
		coriacea	Southern Australia
		denhartogii	Southern Australia
		kirkmanii	Southern Australia
Hydrocharitaceae	*Enhalus*	*acoroides*	Indo-West Pacific and Australia
Thalassioideae	*Thalassia*	*hemprichii*	Australia
		testudinum	Caribbean and Florida
Halophiloideae	*Halophila*	*ovalis*	Global
		ovata	Trop. Australia, Southeast Asia
		minor	Australia, SE Asia, Western Pacific
		australis	Southern Australia
		hawaiiana	Hawaii
		madagascariensis	Madagascar
		johnsonii	Florida
		decipiens	Australia
		capricorni	Queensland and New Caledonia
	Halophila sect. Microhalophila	*beccarii*	India and SE Asia
	Halophila sect. Spinulosa	*spinulosa*	Tropical Australia, Indonesia, and Philippines
	Halophila sect. Tricostatae	*tricostata*	Tropical East Australia
	Halophila sect. Americanae	*engelmannii*	Gulf of Mexico and Caribbean
		baillonii	Caribbean
Ruppiaceae	*Ruppia*	*tuberosa*	Australia
Zannichelliaceae	*Lepilaena*	*marina*	Southern Australia

The taxa regarded as seagrasses belong to four families, viz., the Zosteraceae, the Cymodoceaceae, the Posidoniaceae, and the Hydrocharitaceae. The first three families contain only seagrasses, but the Hydrocharitaceae contains only three genera that are considered seagrasses. The other 14 genera are confined to freshwater habitats. Two other families contain one species each, and these have not received a lot of research – *Ruppia tuberosa* and *Lepilaena marina* (Table 1). Nine of the 13 genera are dioecious.

Sculthorpe (1969) gave a very comprehensive description of the morphology, physiology, and ecology of submerged aquatic plants in his definitive book. Seagrass plants have adapted to being supported by water and have nonfunctional stomates; they assimilate dissolved CO_2 by diffusion through the epidermis which is the major site for photosynthesis, in contrast to terrestrial plants. Seagrasses vary in their ability to grow in low-light conditions. Most species of seagrass are adapted to lower light levels, and they have evolved gas storage organs, both of which can be considered adaptations that allow them to photosynthetically assimilate CO_2 at low, but sufficient rates. Seagrasses have a thin cuticle over the leaf blade and are halophytic in their physiological traits. Most can live for short periods in a wide range of salinities; the salinity of coastal seawater is about 35 parts per 1,000. Seagrasses also withstand a wide range of temperatures in the coastal waters and are capable of acclimating to seasonal and spatial variability in this environmental factor. *Zostera marina* was found to be growing healthily under ice in an embayment of the Bering Sea. Furthermore, it was living there in anaerobic conditions. Thus, these plants are quite robust in their adaptive potential! Seagrasses have become anatomically adapted to limited access to oxygen by developing aerenchymatic tissues with continuous air-filled lacunae running from leaves to roots. Oxygen is only lost to the water column during the day, but it is continuously lost from roots and rhizomes to the sediment. The oxygen produced in photosynthesis is stored in lacunal spaces of the leaves and can be recycled for use in a limited and localized rate of aerobic respiration. The loss of oxygen to the rhizosphere from root surfaces is vital to protect root tissues by oxidizing reduced toxic phytotoxins like iron, manganese, and sulfide. The oxygen released to sediments has important implications for the degradation of organic matter, acting as the terminal electron acceptor in the oxidative breakdown of organic molecules.

Seagrasses may be monoecious or dioecious. Pollination in the seagrasses takes place in the water column except in *Lepilaena* and *Enhalus* where pollen is released at the surface. In *Enhalus* the male flower breaks the surface and releases the floating pollen to the receptive female flower, and a number of seeds mature in a fruit that may be 5–10 cm long. The seeds germinate on release (McConichie and Knox 1989).

Seagrass ecosystems grow in coastal waters from intertidal to 50 m deep or more. This is an important statement to make at the beginning of a chapter on seagrass ecosystems. Seagrasses are limited in their distribution by light, and 50 m is about the limit that suitable light can penetrate even the clearest coastal waters. Seagrasses require an underwater photosynthetic irradiance more than 11 % of that incident on the water surface. Light is reduced by turbidity in the water, and this turbidity is determined by the content of sediment or organic matter. Light is also reduced by animals or plants growing on the seagrass plants; these epiphytes, as they are called, can often shade seagrass plants to below the photosynthetic compensation point required to sustain plants, leading to death under high nutrient conditions.

Most temperate seagrasses are seasonal having a strong growth in spring and early summer then declining in productivity in fall and winter. In a *Posidonia australis* bed growing in Port Hacking, New South Wales, Australia, the relative growth rate measured as mg of carbon per gram of leaf per day closely followed water temperature (Fig. 1). There is a steep increase in relative growth rate at the beginning of spring to a maximum at the end of summer. When the mean weight of

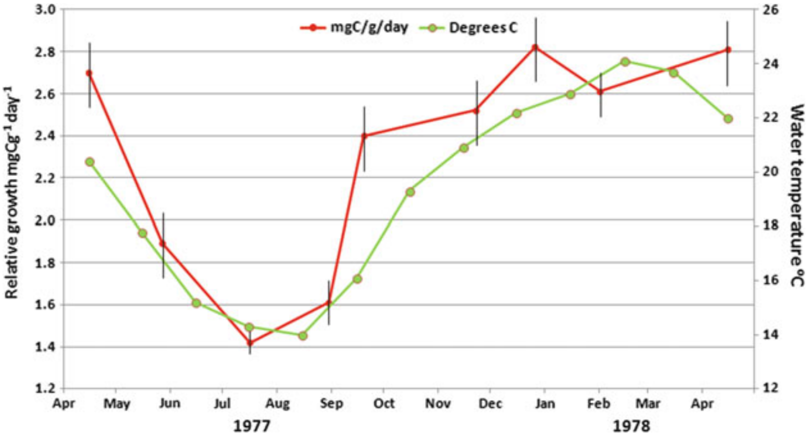

Fig. 1 Average relative growth of *Posidonia australis* leaves from April 1977 to April 1978, with surface water temperature over the seagrass bed. Vertical lines are standard errors about the mean (Kirkman and Reid 1979)

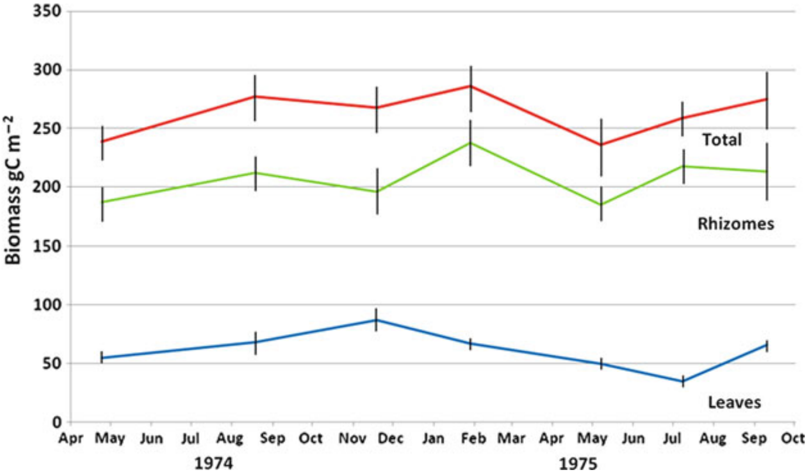

Fig. 2 Dry weight biomass of *Posidonia australis* estimated for a 15-month period. Vertical lines represent one standard error about the mean (Kirkman and Reid 1979)

leaves and rhizomes were charted separately for 15 months, there was not such a seasonal influence as there was in productivity (Fig. 2). These biomasses were the means from ten quadrats each of 0.0625 m^2. These records are important because they represented measurements that could be used for monitoring seagrass condition. Obviously productivity is a more sensitive measurement to detect changes. Unfortunately these measurements are more difficult to make in the field than biomass measures, and we found later that, for large-leaved plants, shoot density was a better measure to determine changes in seagrass condition. Shoots are considered to be a collection of leaves coming from a single node of the rhizome.

Along the tropical and subtropical coasts of Northeastern Australia, the Caribbean, Southeastern USA, Eastern Africa, and Southeast Asian grows a diverse and extensive assemblage of seagrass. These tropical seagrasses growing along continental coastlines are subjected to greater natural disturbance than those in temperate areas. Greater frequency in tropical cyclones, monsoonal extremes in seasonal freshwater runoff into coastal estuaries, and, in tropical Australia, tides to 9 m are not conducive to the establishment and growth of seagrasses. Some tropical seagrasses recover after storms or disturbance quite rapidly, within a year or so, while temperate seagrasses take longer to recover and therefore are not as resilient to disturbance. The well-established concepts of temperate seagrass ecology and habitat function are not appropriate to the diverse range of seagrass habitats in tropical Australia and parts of Southeast Asia. Seagrasses are smaller, are more ephemeral, and have more natural disturbance from dugongs, turtles, and cyclones than do temperate seagrasses. In the tropics *Halophila ovalis* regenerates by vegetative propagules — its rhizomes – while other species set many seeds. Reproductive capacity, in general, is high in tropical seagrasses. Thus, while disturbances to tropical seagrass ecosystems may be more frequent and of greater intensity, they also have greater capacity to recover following those disturbances.

In Darwin Harbour in the Northern Territory of tropical Australia, two species dominate but are ephemeral with cover changing seasonally and distribution also being variable within a year. *Halophila decipiens* and *Halodule uninervis* grow to a depth of about 4 m, but biomass and percentage cover are impossible to estimate by conventional methods due to the variability of observations. Video transects were used to assess seagrass cover and distribution. Thousands of hectares disappeared during the wet season and were replaced in the dry season. Predictions as to how much and where were not accurate. It is believed that the seed bank for each of these lies in the sediment through the wet season (July to January) when light is below compensation level and seeds germinate in April for the dry season where they grow, flower, and set seed until September/October. The waters surrounding these habitats have a very low nitrogen concentration, and the ecosystems are subjected to high disturbance.

Carruthers et al. (2002) identified four broad categories of seagrass habitat. They defined them as “River estuaries,” “Coastal,” “Deep water,” and “Reef” controlled by terrigenous runoff, physical disturbance, low light, and low nutrients, respectively.

In tropical regions seagrass is eaten by manatees, dugongs, and turtles; in contrast, in temperate seagrass beds some swans, geese, and ducks are important consumers of intertidal seagrass. The realization of the biological importance of seagrass was highlighted in the 1920s when large areas in the USA and Europe died causing a decline in commercially harvested fish and shellfish.

In the USA the bay scallop, *Argopecten irradians*, fishery in North Carolina and Chesapeake Bay collapsed following the eelgrass wasting disease of 1931–1932 that destroyed more than 90 % of seagrass. The scallops returned as eelgrass recovered in North Carolina but not in Chesapeake Bay. In southern Florida, in the late 1980s to early 1990s, the pink shrimp, *Penaeus duorarum*, declined by 50 % when there was a 20 % loss of *Thalassia*, the main nursery (from Butler and Jernakoff (1999), Chap. 2).

Seagrass Ecosystems

Seagrasses have diversified and spread to become dominant organisms throughout the world's shallow sediment bottoms around all continents except Antarctica, primarily in estuaries and more sheltered coastal seas. Two genera (the northeastern Pacific *Phyllospadix* and the temperate southern "sea nymph," *Amphibolis*) have even colonized rocky shores. Colonization by seagrasses profoundly changed the nature of coastal sediment systems.

Aboveground, the often dense vegetation strongly reduces the physical energy of waves and currents, creating a zone of kinetic stability within which animal communities can thrive; in addition, it provides food for herbivores and physical structure that shelters a much higher abundance and diversity of animals than do the surrounding bare sediments. The refuge value of seagrasses generally rises with its species or density complexity. Seagrass leaves provide a substratum for growth of epiphytic microalgae and sessile invertebrates and macroalgae that fuel complex food webs. This combined productivity of seagrasses and associated algae ranks seagrass beds among the most productive ecosystems on earth (Table 2).

Moreover, because much seagrass production ends up in belowground tissues and ungrazed detritus, seagrass beds are an important global sink for carbon, accounting for an estimated 15 % of net CO_2 uptake by marine organisms on a global scale, despite contributing only 1 % of marine primary production. Tropical seagrasses tend to support higher metabolic rates and somewhat lower net community production than temperate ones. The production-to-respiration ratio tended to increase with gross primary production exceeding 1 on average. It has been estimated that for a low global seagrass coverage of 300,000 km^2 from 20 to 50 Mt of carbon per year and for a high seagrass coverage of 600,000 km^2 from 40 to 100 Mt of carbon per year (Duarte et al. 2010) has been taken up.

Seagrass beds provide important nursery areas for juvenile fish including commercially and recreationally used fish and shrimp. For example, in the Gulf of Carpentaria in Northern Australia, juvenile *P. esculentus* (tiger prawns) live in seagrass beds and reach sexual maturity at a carapace length of around 32 mm. Although seagrass biomass in the Gulf of Carpentaria was not a consistent linear predictor of juvenile tiger prawn numbers, mean catches of both the 2–2.9 mm carapace length postlarvae and juvenile *P. esculentus* were highest when the biomass of seagrass exceeded 100 g m^{-2}. However, these high-biomass seagrass beds contribute only 6 % to the total extent of seagrasses in the shallow waters (<2.5 m deep) of the Gulf of Carpentaria. Although the numbers of juvenile tiger prawns were lower in the low-biomass seagrass beds, because of their extent, these seagrass beds are the main nurseries for sustaining the production of the valuable

Table 2 Comparison between average seagrass and other marine and terrestrial ecosystems. Net primary production (NPP) (Modified from Mateo et al. (2007))

Ecosystem	NPP (gCm^{-2}/year)	Total global NPP (PgC/year)
Mangroves	1,000	1.1
Seagrass	817	0.49
Forests	400	16.4
Macroalgae	375	2.55
Crops	350	5.25
Terrestrial	200	29.6
Phytoplankton coastal	167	4.5
Phytoplankton ocean	130	43

Northern Prawn Fishery in Australia (production of all prawns in the Northern Prawn Fishery was nearly $28.5 million or 1,627 t in 2011).

The strong network of underground rhizomes found in seagrass ecosystems stabilizes otherwise mobile sediments and filters overlying water by slowing it to allow organic matter and sediments to deposit locally, rather than being washed further offshore. Seagrass beds are nutrient sinks, accumulating detritus from the organic matter deposited in them. Nutrient cycling between sediment organic matter and seagrasses is loosely coupled in time as anaerobic decomposition is slower than aerobic decomposition. Internal cycling of nutrients in seagrass beds comes from seagrass detritus, the animals that live in it and those that ingest seagrass above- and belowground parts.

Seagrass habitats grow naturally as patches in many ecosystems, though they often form continuous coverage under ideal, conditions with rare disturbance. The area covered by them may be stable over decades under some environmental conditions. Increased stresses due to eutrophication and mechanical disturbance from storm surges have the potential to change communities from continuous to fragmented seascapes. Changing from continuous cover to a fragmented seascape may induce positive feedbacks that increase vulnerability of these systems to even further biophysical degradation. Fragmentation of coverage has the potential to cause collapse of food webs, decrease the potential for reproductive continuity within plant and animal populations, and generally threaten biological diversity. The major abiotic factors affecting seagrass seascape structure are the following: physical disturbance from storm and wind-driven waves, the hydrodynamics surrounding the seagrass bed including how well it is protected from storms, water flow around the bed usually from tidal currents, and the size and amount of particle deposition into and around the bed including sediment that drops out of the water column and causes turbidity to increase. Biotic factors are the following: successful recruitment of propagules, clonal reproduction by vegetative propagules, herbivory by animals that eat seagrass leaves, and the abundance and diversity of associated species that rely on seagrass and provide some assistance to seagrass, e.g., animals that break down detritus. The success of predators living on seagrass grazers or on the animals and plants that live on the leaves and stems depends on a complex statis that may not be there when seagrass beds are fragmented. Patches of seagrass may not have the resources available that provide for a stable ecosystem. Nutrient cycling and availability may not be as concentrated as they were in an entire unfragmented bed, producing areas that decline below the size that can withstand storms and wave surges.

Seagrass Morphology

Seagrasses are rooted plants, and many form dense mats of rhizomes in the underlying sediments which reduce the mobility of those sediments and thus stabilize components of local biogeochemical cycles. Roots are not usually supportive organs but have root hairs of variable size and density. The roots of seagrasses are adventitious and grow from the lower surface of the rhizomes, generally at the nodes. Seagrass rhizomes are usually herbaceous and monopodially. Monopodial branching occurs when the terminal bud continues to grow as a central leader shoot and the lateral rhizomes remain subordinate or irregularly branched; however, in *Amphibolis* and *Thalassodendron* the rhizome branches sympodially and becomes woody. Sympodial branching occurs when the terminal bud ceases to grow (usually because a terminal flower has formed) and an axillary bud or buds. Rhizomes are almost always buried in the sediment, and the persistent fibrous remains of old leaf sheaths usually cover the rhizomes of *Enhalus* and *Posidonia* and partially cover the rhizomes in some other genera. The coverage of decomposing leaf sheaths on rhizomes likely provides protection from physical damage as rhizomes are abrased by sediment movement. The leaf is produced either from the rhizome nodes, normally from the upper side in *Enhalus*, *Posidonia*, and the Zosteraceae, or from the apex of erect stems in Thalassia and the Cymodoceaceae. The leaf sheath is clearly differentiated from the leaf blade and encloses the young, developing leaves in all seagrass genera with ribbon blades. *Thalassia* and *Amphibolis* leaves and sheaths abscise together. Leaf sheaths also provide unique protective microhabitats for small invertebrates and their larvae.

Economic Goods and Services Provided by Seagrass Ecosystems

The economic value of seagrass ecosystems has not been well documented. This may be because of the difficulty in defining the goods and services that come from a seagrass bed and then putting a value on the services. “Ecosystem services are the direct or indirect contributions that ecosystems make to the well-being of human populations” is one of many definitions used by economists to value estuarine and coastal resources.

The seagrass ecosystem resource is very valuable when considering the goods and services mentioned above, as a nursery for many species valued by the seafood industry, as a global carbon sink, for nutrient cycling and water purification and to physically stabilize coastlines. Many authors have used generic financial figures to estimate the value of ecosystem goods and services of seagrass beds; but, practically, they vary so widely and have such broad uncertainties when considered together that it is better to gain specific value estimates for specific sites.

Even at the site scale, there is still a large number of ecosystem services that have either no or very unreliable valuation estimates. The most significant problem faced in valuing ecosystem services, including those of seagrasses, is that very few are marketed. Some of the products arising from seagrasses, such as raw materials, food, and fish harvests, are bought and sold in markets; it is easiest to place financial value on these products.

However, the valuation process, even for these products, is more complicated than it first appears. For example, one important service of seagrass beds is the maintenance of fisheries through providing coastal breeding and nursery habitat. Although many fisheries are exploited for commercial harvests sold in domestic and international markets, studies have shown that the inability to control fishing access and the presence of production subsidies and other market distortions can impact harvests, the price of fish sold, and, ultimately, the estimated value of the seagrass habitat in supporting commercial fisheries (Barbier et al. 2011). There is a need for more financial models that include higher-order economic connections and feedbacks in order to more accurately estimate the values of seagrass ecosystems. It is likely that human behavior in both financial and regulatory arenas will have to be added to such models, making it crucial that ecologists' work with economists and social scientists to develop novel modeling frameworks.

Hydrodynamics and Resilience in Seagrass Ecosystems

Seagrass species often sort themselves into assembled communities according to hydrodynamic regimes, e.g., *Amphibolis* spp. and *Phyllospadix* spp., growing in areas of higher flow, compared to other species, in Australia and the East Pacific, respectively. In *Phyllospadix*, reduction of vascular bundles and the absence of woody or cork material allows the leaves to remain erect in the face of strong water action and mechanical stress. It is also more securely attached to its substratum, probably due to greater density in root hair growth, than many species from weaker hydrodynamic regimes. The roots and rhizomes of *Phyllospadix* also have thicker outer epidermal walls, making it better able to withstand strong wave force. The lacunae (internal air spaces) are reduced in volume in this genus, because the plants live in a highly oxic (oxygen-rich), well-mixed environment. Reduced lacunar volume likely provides for greater strength in stems. As would be expected for a plant that needs to be adapted to water motion in a turbulent surf zone, *Phyllospadix* shows more flexible (non-lignified hypodermal) leaf tissues than does *Zostera*, a species from less turbulent environments.

For *Amphibolis* a different adaptation has allowed it to grow in areas of high water movement. It has a characteristic stem and leaf cluster morphology that presents a gap in the canopy, allowing water to flow beneath the main canopy. By contrast, *Posidonia* plants have a uniform leaf shape, maintaining the same leaf width from base to tip (although an increase in canopy density will occur as leaves emerge from their sheaths). This means that there is no gap for water to flow through and hence results in a smoothly decreasing water velocity profile. In the genus *Posidonia* there are two distinct groups: the *australis* group and the *ostenfeldii* group. The *australis* group has stout underground rhizomes that grow laterally in the sediment. This allows them to spread into unvegetated areas, but they do not have the strong hold on the sediment that is exhibited in the *ostenfeldii* group. This group can grow in strong swells and has a typical windrow appearance due to the fact that its seedlings only grow successfully on the lee side of sand ripples. When establishing, the seedlings of members of this group grow as a clump because their rhizomes grow downward once they have established on the lee side of the sand ripples, unlike the lateral pattern of growth in the *australis* group. Gradually the clump enlarges until it coalesces with others, and a full cover is achieved. The leaves of this group are also noticeably stronger than those of the *australis* group.

Exposure to hydrodynamic energy is widely considered an important environmental factor influencing seagrass species distributions; however, its influence compared to other mechanisms has not been tested in many places, and this generalization needs broader consideration. Recently, Hansen and Reidenbach (2013) have shown the importance of *Zostera marina* in reducing velocities of water over them by 60 % in the summer, when leaves were longer, and 40 % in winter compared with an unvegetated site. The seagrass bed also dampened wave heights in all seasons except winter when leaves were shortest. Shear stress was reduced in the summer so that less sediment was resuspended and plants had more light for photosynthesis. Suspended sediment was enhanced by low seagrass coverage in winter compared with an unvegetated site.

Hydrodynamic processes also influence the dispersal of seagrass seeds and vegetative fragments, as well as eggs and larvae of organisms that inhabit seagrass communities and form associated food webs, e.g., invertebrates and fish. Seagrasses baffle unidirectional tidal and oscillatory (wave-driven) currents. Plant morphology and structure affect the capacity of seagrasses to influence water flow. The capacity of seagrasses to baffle water flow and currents is linked to the accretion of sediments and increases with increasing patch structure and size. This, in turn, improves conditions for seagrass growth and recruitment, accelerating patch density and the extent of coverage. Empirical studies of temperate seagrass responses to hydrodynamics, however, have been limited to *Posidonia* spp. and *Amphibolis* spp. in Australia and *Zostera marina* in temperate USA and Europe. There is room for much broader consideration of these potential adaptations and influences on multi-trophic dynamics.

Tidal height and range influence variability in biomass and productivity in intertidal seagrass populations, e.g., those of *Zostera muelleri* in Victoria, Southern Australia, and *Halophila decipiens* and *Halodule uninervis* in turbid tropical waters of great tidal range. Low water levels (tidal heights), barometric conditions, and high temperatures can prompt prolonged atmospheric exposure and desiccation for intertidal species which may result in dieback (Seddon et al. 2000). Empirical studies on the response of seagrasses to atmospheric exposure are limited.

Seagrass Grazers

Waterfowl are significant grazers of seagrasses consuming large amounts of rhizomes and leaves. Swans (*Cygnus atratus*) in Australia eat *Zostera muelleri* while migratory herbivores such as brant geese (*Branta bernicla*) live between the Atlantic coast of the USA from Maine to Georgia, in Alaska, California, and Mexico and feed on seagrass. In the Gulf of Mexico redhead duck (*Aythya americana*) eats *Halodule wrightii*. Swans ingest the rhizomes and leave the leaves to float off, thus affecting spatial patterns of decomposition. Dugongs (*Dugong dugon*) pull out the small plants of *Halophila*, *Cymodocea*, and *Halodule* and, in Shark Bay, Western Australia, eat *Amphibolis antarctica*. Dugongs leave circuitous trails in seagrass beds they have grazed, once again producing the potential for unique spatial patterning in community and ecosystem processes; this is considered as the possible basis for ecological interactions and stimulates seagrass growth. The green sea turtle, *Chelonia mydas*, eats seagrass and macroalgae in tropical seas. They tend to graze in “grazing plots” of *Thalassia testudinum* in the Bahamas choosing young leaves by consistent cropping. There is more digestible forage – higher in protein and lower in lignins – than ungrazed older leaves. Small fish may eat seagrass leaves, fruit, and seeds, and some small grazers, such as snails, and amphipods eat leaf tissue. Because the assimilation rate is quite low, large amounts are returned as detritus and broken down by bacteria. This interaction of vertebrates, invertebrates, bacteria, and seagrass will affect seagrass growth patterns. Some invertebrates ingest seagrass leaves, for example, leaf mining linseed isopods were found in *Posidonia* leaves with more than 90 % of leaves containing burrows. The isopods consumed mesophyll tissue and cells of the vascular bundles (Brearley and Walker 1995).

Epiphytes and Epiphyte Grazers

Seagrass leaves provide a substratum for growth of epiphytic microalgae that fuel food webs and provide shelter for invertebrates and fishes. Mostly, the grazers on seagrass leaves eat epiphytes growing on the leaves (Fig. 3). To predict the impact of grazer-epiphyte interactions, a detailed knowledge of the main processes taking place on several spatial and temporal scales is required. Results cannot be extrapolated from one site to another, and knowledge of recruitment dynamics, the influence of species and morphology of seagrasses on epiphytes and grazers, and the dietary requirements of grazers must be determined for a full understanding of these complex interactions (Jernakoff et al. 1996).

Epiphyte biomass is enhanced by eutrophication more than seagrass biomass, providing the potential for greater optical depths of epiphytes on leaf surfaces and greater extinction of the photon flux required to drive seagrass photosynthesis. Indications of eutrophication may be excessive growth of green and red macroalgae such as *Ulva*, *Enteromorpha*, and *Gracilaria*; algal blooms of phytoplankton can also appear. In the marine environment it is nitrogen that is most limiting, so

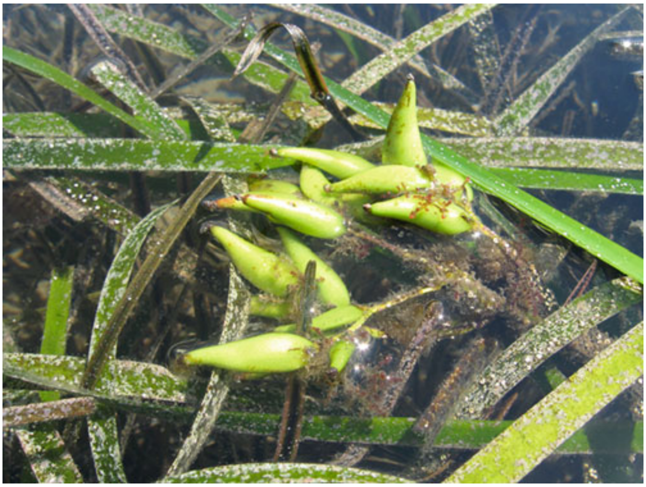

Fig. 3 *Posidonia australis* fruits, note the epiphytes of macroalgae and calcareous polychaetes on the healthy seagrass leaves (Photograph: H. Kirkman)

increased nitrogen stimulates opportunistic algae. The nitrogen, as nitrate and ammonium, enters coastal ecosystems through agricultural runoff, untreated sewage, urban runoff, and land-based pollution that are washed into rivers. The resulting macroalgal blooms that form in eutrophied waters may also form floating rafts, forming an optical filter over beds of underlying seagrass. Another factor that affects the load of epiphytes on seagrass leaves is self-cleaning by the leaves brushing against each other when there is water movement. Epiphytes will accumulate more on seagrasses with stems such as *Amphibolis* and *Heterozostera nigricaulis*, because the stems have been in the water column longer than the leaves. Older leaves will attract more epiphytes than younger leaves.

Complex Food Webs Associated with Seagrass Ecosystems

Epiphyte grazers are part of a complex food web starting with the primary producers – the macroalgal and microalgal epiphytes. There may be hundreds of species of macroalgae on seagrass leaves and stems. Borowitzka et al. (1990) found over 150 species of multicellular algae and over 40 species of sessile invertebrates growing epiphytically on *Amphibolis griffithii* at three widely spaced sites in southern Western Australia. The plant epiphytes are grazed by a multitude of small invertebrates including snails and amphipods. These invertebrates are preyed on by other snails, fish, isopods, and starfish. The grazing fish are preyed on by octopus and larger fish which may be eaten by yet larger fish, sharks, seals, and humans. At the same time the seagrass leaves and aboveground parts are used for protection from predators by many organisms. The pipefish (*Stigmatopora argus*) is well camouflaged in *Posidonia* leaves (Fig. 4), and there are other

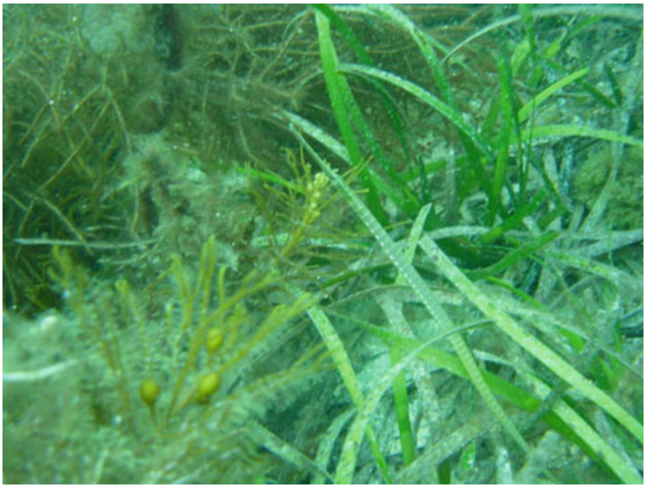

Fig. 4 Pipefish *Stigmatopora argus* on *Posidonia coriacea* (Photograph: H. Kirkman)

invertebrates that are camouflaged, e.g., isopods, snails, and nudibranchs. Juvenile shrimp use seagrass beds as nursery areas, and the tiger prawn (*Penaeus monodon*) in the Gulf of Carpentaria in Australia is only caught in seagrass beds.

The effects of overfishing on seagrass beds can be quite devastating. A top-down trophic cascade can occur when the top-level predators are removed. The decline in large predators brought about by fishing causes an increase in small-fish predators which deplete populations of mollusc and crustacean grazers that normally reduce epiphyte loads. Thus, excessive fishing of some upper trophic level fish has the potential to cause cascading effects down the food web, which ultimately decrease productivity in the primary producers. This process may have more steps in a complex food web, but the end result is that seagrass leaves are smothered by epiphytes reducing the light falling on the seagrass leaves, and if the available light falls below the compensation point (the light level required to sustain a positive carbon balance in the plant), the plants will eventually die (Heck and Valentine 2007). The threat of a trophic cascade caused by recreational and commercial fishing should always be considered.

Under pristine conditions, the older the leaves the more epiphytes there are. In temperate regions, plants like *Posidonia* and *Amphibolis*, which have longer leaf retention times, may hold more epiphytes than the shorter-lived leaves of *Halophila*. Similarly, in the tropics *Enhalus* will hold more epiphytes than *Halodule* or *Halophila*.

The prolific diversity and abundance of motile, epibenthic, invertebrate fauna found in seagrass beds can be illustrated by beam trawls through the seagrass at night when the animals are above the substrate (Fig. 5). A beam trawl for this purpose is usually a meter wide with a roller to prevent damage to seagrass and has skids to move it easily over the seagrass vegetation. The net is usually 2 mm with a

Fig. 5 The animals from a 50 m beam trawl through a *Posidonia australis* bed at Kangaroo Island in South Australia (Photograph: H. Kirkman)

1 mm cod end. The beam trawl is pulled along the bottom at about 2–3 km/h for 50 m collecting all the animals from 50 m^2. An example of the difference between the abundance and diversity of epibenthic fauna in seagrass and on unvegetated sediment was shown in the Albany harbors in Western Australia. In Princess Royal Harbour 18, 50 m beam trawl samples on unvegetated sand caught 258 individuals from 23 species, whereas nearby, in a *Posidonia australis* bed, 3,923 individuals were caught from 68 species (Kirkman et al. 1991). The species collected were amphipods, fish, isopods, molluscs including octopus and squid, and sea cucumbers, brittle stars, and starfish in the echinoderms.

The effect of human impacts on food webs is described by Coll et al. (2011) for temperate Atlantic seagrass beds. They found that the food-web structure was similar among low-impact sites in Eastern Canada and a tropical seagrass web suggesting consistent food-web characteristics across seagrass ecosystems at different latitudes.

Threats to the Future Vitality of Seagrass Ecosystems

Lack of light is most likely the main cause of global seagrass loss. There are several reasons for reductions in light in seagrass beds. Low light at the deeper edge of a seagrass bed is usually caused by turbidity in the water column, which stirs sediments and thus sets a limit to the depth at which the seagrasses can grow. Observations of dynamics in the position of the deeper edge of a seagrass community can be used to describe a great deal about the condition of the seagrass bed and its susceptibility to water quality. At the shallower edge prolific growth of epiphytes will shade seagrasses and reduce their potential for growth and biomass maintenance. Once again, observations of dynamics in the state of the epiphytic cover can be used to track ecosystem vitality over time. Either the epiphytes can be monitored regularly or the border of the seagrass bed can be progressively marked and recorded. These simple measurements at the outer and inner boundaries of the seagrass bed will assist with management.

Human impacts on seagrasses are well discussed in Ralph et al. (2007). Runoff from land clearing in preparation for housing and urban construction may be the largest impact on offshore seagrass meadows. The problem is that the land is cleared for building and sometimes heavy rains wash off the topsoil because it is no longer held by vegetation. New roads and cuttings for roads are another source of sediment runoff. Both of these influences will affect water turbidity and the potential for seagrass growth by threatening light penetration to the seagrass beds.

In Western Port, Victoria, Australia, beds of the subtidal *Zostera muelleri* have been progressively reduced in coverage for the past 50 years. The causes are difficult to remediate. Erosion from clay cliffs and the shore generally and runoff from streams and drains have put sediment into the water column. The continual loss of seagrass has given rise to larger areas of unvegetated mud which is disturbed in rough weather thus adding to the suspended solids and increasing turbidity. Reducing erosion from the cliffs is expensive. Terrestrial runoff is due to poor farming practices and considerable urban development in the catchment and the loss of vegetated stabilized area continues to exacerbate the problem. Attempts are being made to grow mangrove as a sediment stabilizer outside the boundary of seagrass beds and thus reduce wave energy causing erosion.

Development of the coast by building causeways and shoreline armoring may divert water and generally destabilize beaches and shorelines. Rivers are often diverted or changed to enable the extraction of freshwater, and this may have an effect on seagrass beds by favoring one species that prefers seawater (*Heterozostera tasmanica*) over *Zostera muelleri* that has adapted to changed salinity conditions.

Physical damage to seagrass beds can occur when marinas, jetties, and boat ramps are built on or adjacent to seagrass beds, or these structures may change the dynamic hydrology (water circulation patterns) of the area, reducing onshore drift and water flow. Onshore drift is the gradual lateral shift along a beach of beach material resulting from waves meeting the shore at an oblique angle. Mining or oil and gas extraction from under seagrass beds are potentially damaging when considering freshwater flows, oil spills, and mining accidents that cause collapse of mined areas. Moorings and boat ramps add further problems for seagrass ecosystems. The moorings cut spheres in the seagrass bed by chain movement caused by tides and wind. Boat ramps lead to channels being cut in seagrass beds by boat propellers at low tides when boats are leaving or returning to the ramp. Adequate channel markers and a channel will help to prevent this. The main problem with propeller scouring is that during tidal cycles water washes in and out through these rills and these are eroded to form quite large channels in which seagrass propagules are prevented from colonization.

Human occupation of the coastal zone is accompanied by increased rates of pollution. Industrial chemicals from factories, including heavy metals, petrochemicals, and toxic compounds, are a danger to seagrass ecosystems. These pollutants enter the sea from runoff and storm water drains. Agricultural runoff containing herbicides and insecticides can damage seagrass beds and its associated fauna.

By far the most damaging pollutant in seagrass beds is nutrients. These nutrients promote epiphyte growth that smothers the photosynthetic potential of seagrasses and reduces dissolved oxygen levels to dangerously low levels. In marine systems nitrogen excess is usually the primary culprit. Eutrophication occurs when high nutrient loads, particularly inorganic nitrogen, are taken up by opportunistic macroalgae growing on seagrass leaves. The epiphytes and dead seagrass leaves fall to the substrate and are broken down by bacteria that use up oxygen, and this anoxic sediment gives off hydrogen sulfide that kills the benthic flora. The whole seagrass ecosystem may then collapse. Food-web structure and functioning of seagrass habitats change with human impacts, and the spatial scale of food-web analysis is critical for determining results (Coll et al. 2011). The spatial scale is a relevant issue in food-web ecology in general as food webs are typically assembled in aggregated forms (cumulative or summary webs) due to limited data availability on trophic interactions.

Dredging near seagrass beds increases turbidity, and this may cause a smothering effect as well, especially if silt screens are not used. If the sediment load is very high, the effect of seagrass leaves slowing the surrounding water will cause the sediment to drop out of the water column and smother plants. Dredging should generally be carried out in the season when seagrass is least productive, for example, in temperate regions in winter, after carbohydrates and stored material have been laid down in rhizomes or, in the tropics, in the wet season when seagrass beds may die out due to low light because of high sediment loads caused by terrestrial runoff and disturbance of the substrate. They recover naturally during the dry season.

Globally, disease in seagrasses has not been identified as a major threat. After the dramatic reduction of the seagrass *Zostera marina* in the 1930s in the USA and Europe, recovery was slow and only occasionally has *Labyrinthula zosterae*, a marine slime mold-like protist been shown to cause large-scale losses. The death of seagrasses was attributed to *Labyrinthula zosterae*, but later it was established that the plants were under stress and the disease proliferated because of the low resistance of the seagrasses. Diligent monitoring of seagrass beds will alert managers to conditions that could foster secondary impacts due to disease.

Many of the seagrass beds in the USA and Europe provided insulation material from the leaves of *Zostera marina* in the 1920s. The dried leaves, usually recovered from drift on beaches, were used as insulation in sleeping bags and the walls of houses. Collections of large amounts of drift material may affect the nutrient recycling of seagrass beds. There are numerous reports of the slow rate at which seagrass beds will recover from disturbance. One of these is in Spencer Gulf in South Australia where *Posidonia australis* plants were removed to obtain the underlying fiber. This fiber was from the persistent fibrous remains of old leaf sheaths of *P. australis* and was used in clothing manufacture and for insulation in refrigeration units and steam-heating systems. It is of interest to note that although this mining was discontinued in the 1920s, the scars where dredges removed the fiber are still visible today. This and other evidence from seismic blasting suggests that *Posidonia* spp. beds take decades to recover.

Invasive species are a problem in seagrass meadows in some parts of the world. Of particular note is the damage done by *Caulerpa taxifolia* in *Posidonia oceanica* seagrass beds in the Mediterranean Sea (Meinesz, et al. 1993). Some consideration should be given to other invasive species that may arrive, e.g., *Undaria* and *Asterias* are potential invaders that could pose problems in the future. *Undaria pinnatifida* is an edible kelp called wakame, from Japan, that has invaded seagrass beds and rocky temperate reefs. *Asterias amurensis* is the Northern Pacific seastar also from Japan that removes all organisms from reefs and is also found in seagrass beds.

The full extent of climate change effects on seagrass ecosystems has not yet been demonstrated or predicted. However, given the changes that have been noted to date in ocean temperature, salinity, acidification and aragonite saturation, sea level, circulation, productivity, and exposure to damaging UV light, we can anticipate significant degradative effects due to climate change in the future. Loss of seagrass coverage due to exposure to extremes in sunlight or heat has recently been shown in South Australia (Seddon et al. 2000).

Indirect effects of climate change on seagrass communities could occur due to intensification and increases in the frequency of tropical and subtropical cyclones. As discussed above, storms stir up sediment in shallow seas and hence reduce light to seagrass. Increased storm frequency means that there will be increased turbidity and this may reduce light to lower than compensation levels for marginal meadows at the deeper edge. Increased frequency of storms may also disturb seed beds that normally lie in the sediment, e.g., *Halophila ovalis* and *Halodule uninervis* were lost from Hervey Bay, Queensland, when two very large storms followed each other, the first destroying the seagrass and the second destroying newly germinated seedlings (Preen et al. 1995). It took about 5 years for the area to recover. More intense storms will also increase erosion of edges.

Warmer temperatures and ice cap melting are expected to raise sea levels. For seagrasses this will bring their habitats shoreward. Those seagrasses growing at the deeper edge of their habitat may be lost while the shallower margins will gain coverage. The problem is if development has used those shallower edges to the point that the seagrass can move no further up the shore, large areas will be lost. The building of sea walls, coastal roads, housing to the edge of the sea, and other development must be carefully managed with sea-level rise in mind.

Little is known about the effect of seawater temperature rising, but shifts in distribution are expected. Seagrass plants cannot move as can some invertebrates and fish as the water temperature increases. The success of a slow distributional shift will depend upon the suitability of a new habitat being available, the connectivity between seagrass beds and potential new growth areas, and the dispersal mechanisms of the propagules.

As carbon dioxide rises in the atmosphere, more is dissolved in seawater leading to ocean acidification. In seagrass ecosystems, calcareous epiphytes will be the main victims. The response of calcareous epiphytes to a fall in pH from 8.2 (seawater) to 7.7 in aquaria was a loss of all calcareous algae, and the only calcifers were bryozoans at pH 7.7 (Martin et al. 2008). This result may have dramatic effects on biogeochemical cycling of carbon and carbonate in coastal ecosystems dominated by seagrass beds.

Restoration and Recovery

There is considerable confusion in the natural-resource management field about the terms "rehabilitation" and "restoration." Dictionaries generally tend not to differentiate between the two (e.g., see Shorter Oxford English Dictionary) nor do many learned articles on the creation of new seagrass habitats, but there is a distinction worth making, especially with degraded ecosystems. "Restoration" could mean "*reversion of a degraded ecosystem to its original condition*" or "*inducing and assisting abiotic and biotic components of an environment to recover to the state that they existed in the unimpaired or original state*." This is acknowledged as being an unlikely outcome in practice.

In contrast, "rehabilitation" describes an *acceptable improvement in ecological condition* and, in most cases, is a more realistic management objective. Rehabilitation of degraded, seagrass beds is where management interventions are expected to markedly improve the ecological condition of these systems and allow them to again deliver, in broad terms, the sorts of ecosystem services that humanity expects but are never intended to return the system to some notional "pristine" condition. From rehabilitation one could distinguish three types of management outcomes: (i) maintenance, (ii) improvement, and (iii) reconstruction. In this scheme, reconstruction broadly equates with restoration, and improvement with rehabilitation.

An associated discipline is ecological engineering, which involves restoring and creating sustainable seagrass ecosystems that have value to humans and nature. Ecological engineering should restore/rehabilitate damaged seagrass ecosystems and create new sustainable systems in a cost-effective way.

The term "mitigation" refers to the enhancement or creation of seagrass areas to compensate for permitted seagrass losses. Offsets may be used when a seagrass bed is sacrificed for a shipping channel, land claim, or development that destroys a seagrass bed and the bed cannot be restored or moved somewhere else.

Planting success may be defined in a number of ways. First, sometimes success is claimed if seedlings grow sufficiently to produce their own reproductive structures, and their canopy, covering the area planted, is similar to a nearby unaffected seagrass bed. Second, criteria, preferably measurable as quantitative values, could be established prior to the commencement of planting activities. Success can then be defined as the successful integration of plant material establishment with fishery and wildlife habitat establishment and water quality improvements. This habitat equivalence can be measured with quantitative measures such as species presence in conjunction with plant cover. The habitat measurements are compared with a proximate seagrass ecosystem. A third approach might be to set a numerical target for survival over a given period, e.g., 70 + % survival of planted seedlings or transplants after 1 year.

Environmental offsets are measures to compensate for the adverse impacts of an action on the environment. Offsets do not reduce the impacts of an action: instead they provide environmental benefits to counterbalance the impacts that remain after avoidance and mitigation measures. These remaining impacts are termed “residual impacts.” Offsets are not intended to make proposals with unacceptable impacts acceptable. In assessing the suitability of an offset, government decision making should be informed by scientifically robust information and conducted in a consistent and transparent manner.

More specifically, offsets are measures to compensate for environmental impacts on seagrass ecosystems that cannot be adequately reduced through avoidance or mitigation. Offsets for seagrass ecosystems can help to achieve long-term conservation outcomes for protected areas, while providing flexibility for proponents seeking to undertake an action that will have unavoidable environmental impacts. For example, if a seagrass area is to be dredged or claimed for development, the seagrass that is to be destroyed could be collected and planted somewhere else where seagrass was known to have previously survived and is suitable for restoration.

A major difficulty in restoring seagrass ecosystems is the difficulty of obtaining suitable propagules. Sometimes seeds are unavailable or scarce such as in the genus *Syringodium* in Australia, the USA, and Caribbean or where seeds are plentiful such as in *Zostera muelleri*, in Australia, but the germination rate is low. Some genera produce viviparous seedlings and no seeds are seen, e.g., *Amphibolis* and *Thalassodendron* in Australia. *Posidonia* produces a buoyant fruit (Fig. 3) from which a seedling falls after floating for a few days. These seedlings, although numerous, present problems when attempting to restore large areas. *Posidonia oceanica* does not regularly produce copious quantities of seedlings in the Mediterranean. *Amphibolis* and *Heterozostera* produce adventitious roots from their stems, and these are useful natural propagules when the stems break off the plant and float away to eventually sink in a suitable environment.

Seagrass transplanting is well known for its failure arising from a number of causes, such as planting at sites where seagrass had no history of growing; disturbance of the substrate by burrowing animals (bioturbation), storms, insufficient light, lack of knowledge, and experience by those transplanting; and other local reasons.

In the absence of natural recruitment, sprigs or seedlings may need to be sourced from a donor site some distance away. An understanding of levels of genetic diversity and spatial genetic structure can contribute to improved restoration outcomes by identifying the most genetically appropriate source material for restoration sites.

Genetic Diversity

The poor knowledge of the minimal habitat requirements for seagrass growth, colonization and establishment mechanisms, genetic diversity, and reproductive modes required to maintain ecologically successful populations hinders the development of sound management practices. The development of molecular DNA sequencing techniques over the last decade has provided new tools to examine genetic variability within and among seagrass populations. Much of the power inherent in molecular genetic data can be tapped, revealing otherwise unobtainable information at all levels of biotic hierarchy (Kendrick et al. 2005).

Alberte et al. (1994) assisted with breakthroughs in determining that populations that were morphologically distinct and may have shown different depth distributions could be distinguished by DNA fingerprinting. They also determined that *Zostera marina*, in particular, was not characterized by a high degree of clonal reproduction at spatial scales over 5 m, and they found that *Z. marina* growing in a physically disturbed bay had reduced genetic diversity. Knowing the effect that disturbance has on genetic stability can help establish mitigation and restoration criteria.

Genetic diversity in terms of greater numbers of distinct clones was positively associated with seagrass bed density, and this in turn was correlated with greater invertebrate density, nitrogen retention, and areal productivity. Higher abundances of invertebrates associated with seagrasses in more genetically diverse *Zostera* plots and the positive effects of seagrass genotypic diversity on both seagrass and grazer biomass depended on grazer species identity. Since mesograzers can have strong effects on the biomass of both epiphytic algae and seagrasses, and since seagrass genotypes vary in palatability, understanding the implications of changing diversity in seagrass ecosystems will require more detailed study of genetic and species diversity effects at multiple trophic levels. Nevertheless, the picture emerging from controlled experiments and seagrass restoration projects appears consistent: seagrass genetic diversity may be a key variable influencing seagrass productivity and community processes (Duffy et al. 2013).

There is also a positive impact of clonal diversity along an entire depth gradient on food-web complexity and density and nutrient retention. Ecosystem restoration will significantly benefit from obtaining sources (transplants and seeds) of high genetic diversity and from restoration techniques that can maintain that high genetic diversity (Reynolds et al. 2012).

Seagrasses provide convincing examples of the broader ecological importance of genetic or genotypic diversity. Higher allelic diversity within individuals increased vegetative shoot production and sexual reproduction in transplanted seagrasses, and transplant success correlated positively with the genetic diversity of individuals in the source population (Procaccini et al. 2007). More convincing was the evidence from experimental manipulations of the number of seagrass genotypes (as measured by DNA microsatellites), which demonstrated that genetic diversity within a patch can influence primary and secondary production, particularly in the face of disturbance or stress. Patches of eelgrass (*Zostera marina*) with greater numbers of clonal genotypes were more resistant to seasonal grazing by migratory geese, resulting in increased shoot density after grazing in high-diversity areas and quicker recovery to pre-grazing densities, in the more diverse areas. Genotypic (and thus phenotypic) diversity also increased the rate of recovery from extremely high water temperatures in *Zostera marina* suggesting that this effect may be a generalized response to aboveground biomass removal. Subsequent manipulations that controlled for disturbance confirmed the positive effects of genetic diversity in the presence and absence of disturbance. Thus there is growing evidence, albeit only from *Zostera* so far, that genetic diversity within seagrass species can be important in buffering seagrasses from several types of perturbations. Genotypic diversity can have positive consequences at the community level as well.

It is only recently that one has begun to understand the genetics of seagrass plants and what a seagrass plant is. In Western Australia vast beds of *Posidonia* extend for kilometers along the coast; until now it has not been possible to say how extensive a single plant is. *Posidonia oceanica* in the Mediterranean is one of the largest, slowest growing, and longest-lived plants terrestrially or in the sea. In a recent genetic study of 40 *P. oceanica* populations across the Mediterranean, Arnaud-Haond et al. (2012) found individual clones spanning up to 15 km. Based on the plant's known growth rate, such individuals are likely to be thousands, possibly tens of thousands of years old. This was different from the high degree of clonal reproduction in *Zostera marina* shown by Alberte et al. (1994).

The discoveries made by DNA have also helped untangle some of the taxonomic identities of seagrass. It is at this point that an understanding of levels of genetic diversity and spatial genetic structure can contribute to improved restoration outcomes. Identifying the most genetically appropriate source material for restoration sites can be carried out with DNA analysis.

From molecular studies in combination with ecological and hydrological assessments, it is evident that seagrasses are resilient and have persisted in a physiologically challenging submerged environment because they have broad niches. That local persistence of seagrasses has been achieved by clonal growth and by recruitment from sexually derived propagules. Some seagrasses invest significant amounts of energy in sexual reproduction, producing seeds with a high capacity for long-distance dispersal that enables them to colonize distant new locations (Kendrick et al. 2012).

Future Directions

There is a recent trend for widespread loss in tropical and temperate seagrass ecosystems. Large-scale declines have been reported by Hemminga and Duarte (2000) at 40 locations, 70 % of which are attributed to human induced disturbance. There are some areas that have recovered but the long-term trend is for continual global loss. Short and Wyllie-Echeverria (1996) estimated the area of seagrass lost globally at 12,000 km^2 or about 2 % of the area originally covered. Present losses are expected to accelerate, particularly in areas of Southeast Asia and the Caribbean where human pressure is greatest and development incentive is greater than environmental conservation. Restoration of seagrasses seems to be the greatest challenge facing ecologists. Efforts to restore seagrass need to be based on knowledge of local conditions, the ecological state of the system prior to disturbance, and informed decisions about what should be there after restoration. The genetic investigations into clonal seagrass identity may be helpful in restoration efforts.

It is difficult to separate natural variability from human-caused disturbance. The role of disturbance and the response by seagrass species to a particular disturbance should be a major focus of long- and short-term research. Now that climate change is a component of disturbance, the investigation has become even more complex. It is recommended that monitoring of seagrass to distinguish between these causes and to answer relevant questions on management of seagrass ecosystems be carried out.

As concern increases for the state of natural resources and the degradation of the world's oceans, it is critical for countries to progress with conservation actions specifically focused on seagrass ecosystems. Guidelines for Applying the IUCN Protected Area Management Categories to Marine Protected Areas (MPA) aim to make clear what is most significant and of highest priority, and this effort will help countries more accurately detail their successes (www.iucn.org/pa_guidelines). These guidelines will define MPAs thus preventing the trend of fisheries advisory bodies claiming that area mechanisms exploiting fish are MPAs. About 50 % of global MPAs are considered to have been wrongly allocated because the name of the MPA, e.g., National Park and Sanctuary, has been used to determine the category, rather than the management objectives. Confusion tends to arise when sites have been incorrectly assigned on the basis of activities that occur, rather than using the stated management objectives. In recent years pressure to deliver success stories has resulted in false claims of large areas of seagrass being properly protected. It is time to be realistic about our definition of MPAs in seagrass ecosystems.

Protecting seagrass beds through education of local communities and fishers and by regulations and even enforcement will help conserve this valuable resource. Properly regulated marine protected areas will assist with conserving seagrass ecosystems with benefits to conserving biological diversity and spillover advantages to nonprotected areas.

It is time to stop pretending more areas of seagrass are protected than they actually are. Understanding which seagrass beds are protected and how they are protected is of paramount importance in promoting driving global conservation efforts. Without this information it is difficult to hold the process of determining marine protected areas in seagrass ecosystems accountable.

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