Anthony W. D. Larkum · Gary A. Kendrick
Peter J. Ralph *Editors*

# Seagrasses of Australia

## Structure, Ecology and Conservation

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# Preface

In 1989, the Biology of Seagrasses: Treatise on the Biology of Seagrasses with Special Reference to the Australasian Region (edited by Anthony W. D. Larkum, Scoresby Shepherd and Arthur McComb) was published at a time when seagrasses were being recognized as keystone benthic species amongst coastal ecosystems. Australia with 40 of the 70+ species around the world and large seagrass beds in both temperate and tropical sites was clearly a central focus of seagrass biology, both in terms of a knowledge base and source for further research into these unique plants. It was early realized that the 70+ species of seagrasses, an incredibly small number of species compared with the several hundred thousand species of flowering plants, have special features which enabled them to enter the marine environment from which their charophyte green algal forebears evolved in the Ordovician Era (some 500 Mya). And this in itself was enough reason to publish a book on Australian seagrasses, which also comprise a major proportion of the world species and have representatives of every seagrass group.

Seagrasses have continued to dominate the world stage in research, and Australia maintains its leading position on this stage, partly because of the prime role that Australian seagrasses hold, but also because of the exceptional quality of Australian seagrass researchers. Thus, there has been an increasing need to revisit the subject of Australian seagrasses over recent years, and we are very grateful to Springer-Verlag for agreeing to publish a new book on this topic.

In 1989, the editors of that volume drew attention to five important aspects of seagrass biology:

1. The economic significance of seagrasses,
2. The importance of physiological studies and microbial interactions,
3. Population studies,
4. The decline of seagrasses and
5. Conservation studies.

Today, these aspects and further realization of the unique features of these plants continue to influence our thinking on the importance of seagrasses both in a world context as well as the unique Australian context. And these themes too are reflected in the present book, exemplifying the strong research tradition that has passed on to younger researchers in Australia.

Yet, there have been some significant advances in biology that have revolutionized the way we think about seagrasses. These advances have been in the areas of (i) *molecular biology*, (ii) *phylogenetics*, (iii) *global climate change* and (iv) the *blue carbon* aspect of seagrasses. And they have brought about unexpected changes in the way we view seagrasses as well as reinvigorate the original five topics examined in the first edition.

In the area of *molecular biology*, we have seen the ability to carry out a full genome analysis of each species of seagrass. Not just a single assay either, we can now do multiple analyses on a single species. This advance yields extraordinary amounts of information, which, if properly handled, can be used at a number of levels in enhancing our knowledge of seagrasses; however, at this time it must be acknowledged that much of the value lies in the future. Nevertheless, in looking for current examples we can cite taxonomic breakthroughs (Chaps. 1, 5 and 6) specific biochemical pathways in various lineages (Chap. 16) or in understanding the biogeographic range of a seagrass (Chaps. 3, 8 and 9). And in general, this advance has ushered in the era of "*Omics*" which covers everything from the genes and genomes (*genomics*), through *transcriptomics* to *proteomics* and *metabolomics*; this information has filtered through to almost every chapter in this book.

In the area of *phylogenetics*, in conjunction with gene and genomic studies, we have seen sharp changes in our view of seagrass species and their affinities. It has enabled us to understand the evolution of seagrasses, in space and time in a way that was not possible in the first edition (see Chaps. 1 and 5). And in some cases, it will undoubtedly lead to a revision of the accepted species of seagrasses (Chap. 5). Similarly, population genetics, reproduction, dispersal and recruitment and population connectivity have evolved, and our knowledge of both genetic and demographic connectivity has been a focus of research since 2000 (Chaps. 6 and 8).

In the area of *global climate change*, we have seen a vigorous debate emerge in which despite the objections of "climate deniers", we have seen noticeable shifts in climate in many parts of the world with higher incidence of storms, hurricanes and cyclones. On a world scale, we have seen carbon dioxide levels rise in 2016 to 400 parts per million for the first time in many thousands of years (World Meteorological Organization) and the likelihood that it will continue to rise far into the future. In 2015, 195 countries met in Paris at the Twenty-First Conference of the Parties of the United Nations Framework Convention on Climate Change (UNFCCC) and adopted by consensus on 12 December 2015 the Paris Agreement. This is an agreement within the UNFCCC dealing with greenhouse gases emissions mitigation, adaptation and finance starting in 2020. The agreement went into effect on 4 November 2016 and, despite retraction by the Federal government of the USA in Washington, seems set to have a great influence on future carbon use around the world.

Now we have seen how a redefinition of the turnover properties of various plant products has led to a re-evaluation of the importance of seagrasses in our environment. This has brought in the new concept of "*Blue Carbon*"; the realization that carbon deposited in organic form in seagrasses (and salt marshes and mangroves) has a tenfold longer life than that of other plants has increased the respect with which politicians and planners bring to our much threatened seaboard. Much of this work has developed earlier sediment biogeochemistry to address these new policy-driven questions associated with integrating coastal vegetation into greenhouse gas accounting.

Unfortunately, any increased awareness of seagrasses by the public, politicians and planners has been offset by ineluctable desire to build along and out from our beautiful shores and also by the far more insidious but all-pervasive effects of riverine and estuarine pollution and *global climate change*.

*Global warming* in 1989 was viewed by most informed workers in the field as a long way off and something to be mitigated by future tactics. Since those days, it has become apparent to all but a few that climate change is a major, if not the major, problem facing human civilization. One major effect of increased greenhouse gases, especially $CO_2$, will be the rise in temperature of the planet. If this can be kept to no more than a 2 °C rise, it would be possible for most plant and animal communities to survive with little harm (Intergovernmental Panel on Climate Change). Indirect effects through increased violent weather events are already becoming apparent. On the good side of the balance, a warming of the seas by 4 °C would not be disastrous for seagrasses as it is likely to be for reef-forming corals, which are likely to be pushed to extinction. Seagrasses could survive. But in addition to warming of the seas, there is also the effect of *ocean acidification* (*OA*), a subject that was little talked about in 1989. The effect of OA on seagrasses is not well understood, but the few attempts to factor this phenomenon in have predicted strong effects (see Chap. 21).

Putting all these factors into the balance, the future does not look good for seagrasses. And we need a heightened awareness of the threats to seagrasses if we are to conserve them. We also need a much greater public appreciation of the importance of this source of blue carbon in our national greenhouse gas accounts (Chap. 22).

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# Part I
# Biogeography

# Chapter 1
# Evolution and Biogeography of Seagrasses

**Anthony W. D. Larkum, Michelle Waycott and John G. Conran**

**Abstract** Seagrasses are an organismal biological group united by their ability to grow in marine environments. As marine flowering plants they have evolved a combined suite of adaptations multiple times enabling the four known lineages containing species of seagrass to survive, and thrive, in the sea. Unlike many other biological groups of plants however, seagrasses are all derived from a single order of flowering plants, the Alismatales. This order, being derived early in the evolution of the monocotyledons, is comprised predominantly of aquatic plants, of all forms–emergent, submerged, freshwater, estuarine and marine. A review of seagrass fossils suggests that new discoveries of seagrass fossils along with confirmation of some earlier finds lead to a clear signal that some seagrass species had a wider distribution in the past compared with today. The discovery of new fossil sites should be encouraged as this will likely produce important valuable information on the evolution of this group. In general the biogeography of seagrasses suggests that these organisms evolved successfully in the Tethys Sea of the Late Cretaceous. However, the modern division into two groups, temperate and tropical tends to suggest that at some point an ecological separation occurred in both the Northern and Southern Hemispheres. There are a disproportionately large number of temperate seagrass species in southern Australia and there is significant endemism shown in Posidonia, Amphibolis and a unique species of Halophila (H. australis).

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The use of genetic and genomic techniques has begun to explain these distributions but we can expect a much bigger picture to emerge in the near future.

## 1.1 Introduction

Among the higher plants, whose ancestors left the sea some four hundred million years ago, the seagrasses are the only group to have returned to a completely submerged marine existence (Arber 1920; Sculthorpe 1967; den Hartog 1970; Larkum and West 1989; Les et al. 1997). Fossil evidence indicates that angiosperms arose in the late Jurassic (Raven and Axelrod 1974) or early Cretaceous Periods (Thomas and Spicer 1984), at around 140 million years ago (Ma) and molecular clock dating also supports an early Cretaceous or Jurassic origin for the angiosperms (Doyle 2012). The limited fossil record for seagrasses indicates their ancestors, which are the basal lineages of the Alismatales (Refer to Table 1.1 for families included in the Alismatales and following the recent classification published by the Angiosperm Phylogeny Group 2016). This group will be referred to as 'alismatid monocots' or Alismatales, see discussion in Waycott et al. (2016, Chap. 5).), likely evolved more than 100 Ma ago in the Cretaceous Period, modern seagrass families beginning to diverge more than 70 Ma (Anderson and Janssen 2009; Janssen and Bremer 2004; see also Chap. 5). Molecular divergence times across the order Alismatales support these hypotheses that fossil based evidence indicates progenitors to modern seagrasses arose during the mid-Cretaceous (Hertweck et al. 2015; see also Chap. 5). However, the different modern family lineages of seagrasses vary in age and most are considerably younger (Les and Tippery 2013; Waycott et al. 2016, see also Chap. 5). Given such a well-established, long evolutionary history, it is remarkable that although there are several hundred thousand species of angiosperms in existence today there are only some 65 species of seagrasses.

Evidence that there are multiple independently-derived lineages of seagrasses has been well established since the molecular phylogenetic study of Les et al. (1997). The findings of this study, that the alismatid monocots contain within them four, polyphyletic lineages containing seagrasses, provides a framework for the evaluation of the evolution of these groups (e.g. Waycott et al. 2004, 2006, 2014, Chap. 5; Kilminster et al. 2015). The four lineages are (1) the marine Hydrocharitaceae, (2) three families together referred to as the Cymodoceaceae 'complex' by Les et al. (1997) including the Cymodoceaceae, Ruppiaceae and Posidoniaceae, (3) the Zosteraceae and (4) a small number of species in the Potamogetonaceae formally in the Zannichelliaceae. The ecological success of these lineages is significant, seagrasses occupying the nearshore, relatively shallow coastal environments on all continents except Antarctica (den Hartog 1970; Short et al. 2007). In addition, seagrasses are crucial to healthy ecosystems of shallow inshore regions of the world (den Hartog 1970; Duarte 2002; Larkum et al. 2006; Orth et al. 2006; Waycott et al. 2006).

**Table 1.1** Current families recognised in the monocotyledonous plant order Alismatales Dumortier (Angiosperm Phylogeny Group 2016). Genera recognised as seagrasses listed next to family recognised in the order, seagrass families and genera are **bold**

| **Family** | **'Seagrass' genera** | Estimated number of species in family[a] | **APG IV family number[b]** |
|---|---|---|---|
| Alismataceae (including Limnocharitaceae) | | 88 | 30 |
| **Hydrocharitaceae** | | 116 | **32** |
| | ***Enhalus*** | | |
| | ***Thalassia*** | | |
| | ***Halophila*** | | |
| Butomaceae | | 1 | 31 |
| **Cymodoceaceae** | | 16 | **41** |
| | ***Cymodocea*** | | |
| | ***Thalassodendron*** | | |
| | ***Amphibolis*** | | |
| | ***Syringodium*** | | |
| | ***Halodule*** | | |
| **Ruppiaceae** | ***Ruppia***[c] | 10 | **40** |
| **Posidoniaceae** | ***Posidonia*** | 9 | **39** |
| **Potamogetonaceae** | | 102 | |
| (including Zannichelliacae) | ***Lepilaena***[c] | | **38** |
| **Zosteraceae** | | 14 | **37** |
| | ***Phyllospadix*** | | |
| | ***Zostera*** | | |
| Maundiaceae | | 1 | 36 |
| Juncaginaceae | | 30 | 35 |
| Scheuchzeriaceae | | 1 | 33 |
| Aponogetonaceae | | 50 | 34 |
| Araceae | | 4150 | 28 |
| Tofieldiaceae | | 31 | 29 |

[a] Following the Angiosperm Phylogeny Website available via http://www.mobot.org/MOBOT/research/APweb and organized by P. F. Stevens, from 2001 onwards

[b] The numerical designation given to each family in the orders identified by APG IV (Angiosperm Phylogeny Group 2016)

[c] Not always treated as seagrasses although species are tolerant of salinities ranging from brackish to marine to hypersaline salinities

Despite a long evolutionary history, there is a distinct lack of speciation amongst seagrasses, which appears inconsistent with their apparent widespread success (Les et al. 1997; Waycott et al. 2016, Chap. 5). Indeed, the majority of significant diversity in the group occurs among genera (Waycott et al. 2006). Given the poor fossil record and the lack of species diversity within genera it is likely that seagrasses have suffered major extinctions throughout their evolutionary history. Indeed, evidence for this may be seen in the relationship seagrasses have with Sirenia (i.e. dugong and manatee) where, as the major food source (see Chap. 19) their histories have been interlinked. Turtles feed on seagrass leaves alone, whereas Sirenia often feed on leaves and below ground structures. And the evolution of Sirenia seems to have depended on the presence of seagrasses (Domning 1981, 2001; Fitzgerald et al. 2013; Chap. 19). However, it is likely that we will not know much more about the factors involved with speciation in these unusual flowering plants until we know more about the processes of speciation in general (Lockhart et al. 2015) and the genetic variability present within and among seagrass species in particular (see Chaps. 5, 6 and 8).

In this chapter we will discuss:

1. The current evidence of seagrass evolution based on the fossil record;
2. A summary of the current knowledge on the biogeography of seagrasses; and
3. The distribution of Australian seagrass communities.

## 1.2 Fossils and Seagrasses

One consequence of seagrasses being polyphyletic across a long evolutionary history and among multiple alismatid lineages is that identifying seagrass fossils can be problematic. In particular, the determination of fossils as being seagrasses, when found in aquatic fossil deposits when no reproductive structures are detected is a significant limitation (Iles et al. 2015). Here we present a summary of the fossil evidence known for the overall order that seagrasses occur in, the Alismatales and summarise what is known about seagrasses from among the evidence known to date. For reference, the work of Les and Tippery (2013) and Iles et al. (2015) in addition to Les et al. (1997) and Waycott et al. (2006) and the summary presented in Chap. 6 (viz. Waycott et al. 2016) provide details for the wider (and non seagrass) taxonomic groups being discussed. We have adopted here, with respect to higher order taxonomy, the Angiosperm Phylogeny Group IV classification, which provides a listing of all families and orders of the Angiosperms following the latest synthesis (Angiosperm Phylogeny Group 2016).

### *1.2.1 Fossil Record of the Alismatales*

The fossil record of Alismatales has been summarised recently by Stockey (2006), Friis et al. (2000, 2004, 2011), Smith (2013), Conran et al. (2015a) and Iles et al. (2015). There are fossils known from most of the families in the order, but the majority of the reliable records are for freshwater members of this order of monocotyledons. Because of the morphological and anatomical similarities, particularly in leaf blade form, between the marine members of Cymodoceaceae, Hydrocharitaceae, Posidoniaceae and Zosteraceae (Stockey 2006; van der Ham et al. 2007; Benzecry and Brack-Hanes 2008; Smith 2013) they are generally just treated as 'seagrasses' even though they represent several lineages of the Alismatales with convergent exaptation to a submerged aquatic habit (Les et al. 1997; Ross et al. 2015). This is particularly problematic for fossils, where reproductive material is rarely preserved, making their accurate generic, or even family placement extremely difficult in most cases. For reference, go to Chap. 5 (Waycott et al. 2016) to review relationships in the monocotyledon order Alismatales.

### *1.2.2 Alismataceae*

Fossils with similarities to Alismataceae (including Limnocharitaceae) occur from the Late Cretaceous onward (Stockey 2006; Smith 2013), including the genera *Cardstonia* M.G. Riley & Stockey, *Haemanthophyllum* Budantzev and *Heleophyton* D.M. Erwin & Stockey (Erwin and Stockey 1989; Golovneva 1987; Riley and Stockey 2004). These fossils show strong similarities to living Alismataceae, but some also share characters with Aponogetonaceae and Butomaceae and the earliest reliable fossils are late Eocene Alismataceae fruits from the Isle of Wight (Collinson 1983; Hooker et al. 2009) and Northern Hemisphere Oligo–Miocene fossil fruits of the extant genus *Caldesia* Parl. (reviewed in Haggard and Tiffney 1997) and Miocene fruits resembling *Limnophyton* Miquel (Haggard and Tiffney 1997). There are Miocene *Alisma* fossils known from Germany (Mai 2000), but the precise identity of these requires confirmation (Iles et al. 2015).

### *1.2.3 Aponogetonaceae*

Several fossil leaves have been considered to have affinity with Aponogetonaceae, but alternative assignments to other alismatid families are often possible (Smith 2013). The pollen of Aponogetonaceae is distinctive and is known from Late Cretaceous and early Cenozoic sediments from North America and Greenland (Grímsson et al. 2014), with three species referred to different pollen subtypes within *Aponogeton* L.f.

### *1.2.4 Hydrocharitaceae*

Seeds assigned to the extant genus *Stratiotes* L. genera first appear in the late Palaeocene of England (Sille et al. 2006; Stockey 2006; Smith 2013). Additional Eocene to Miocene fossils have also been assigned to modern genera, but most of these require further study (Smith 2013; Iles et al. 2015).

### *1.2.5 Potamogetonaceae–Cymodoceaceae (Incl. Ruppiaceae)*

These worldwide families of submerged to floating aquatic macrophytes have similar, characteristic endocarps that have been found in Cretaceous to Pliocene marshy, lacustrine or estuarine fossil deposits mainly across the Northern Hemisphere, but with some recent Southern Hemisphere discoveries (Collinson 1983; Zhao et al. 2004; Gandolfo et al. 2009; Smith 2013; Iles et al. 2015). However, despite being regarded traditionally as closely related to each other, *Potamogeton* L. (Potamogetonaceae) and *Ruppia* L. (Cymodoceaceae) are only distantly related, *Ruppia* belonging instead to a diverse clade that includes the seagrass families Cymodoceaceae, Posidoniaceae and Zosteraceae (Les et al. 1997; Iles et al. 2015). As a result, although numerous genera have been created for fossil *Potamogeton*- and *Ruppia*-like fruits, their relationships require re-evaluation in the light of these revised family relationships.

Pole (1993) suggested that some long-tailed, short-beaked fruits found in the Miocene Lake Manuherikia fossil deposit represented possible Poaceae, interpreting their elongated tail-like structures as awns. However, re-examination of these fossils showed that the fruits actually represent the first Neogene record of *Ruppia*-like macrofossils for New Zealand (Conran et al. 2015a). *Potamogeton* and *Ruppia* are both dispersed over long-distances by water birds (Green et al. 2002), so it is not surprising that they were present in the paleo-Lake Manuherikia, as diverse water birds were abundant there in the middle Miocene (Worthy et al. 2007, 2008). There are also Pliocene-aged fruits described by Oliver (1928) as achenes of *Clematis obovata* W.R.B. Oliver (Ranunculaceae), which more closely resemble long-stalked *Ruppia* endocarps (Conran, unpubl. obs.) and these are the subject of ongoing research.

The endocarps at Lake Manuherikia occur in close association with abundant (>60%) *Sparganiaceaepollenites* Potonié pollen from several species. This is similar to the Paleogene South American sediments studied by Gandolfo et al. (2009) where *S. barungensis* Harris pollen was recorded in association with fossil *Baibiancarpus* Gandolfo et al. fruits (Potamogetonaceae). That study noted considerable morphological variation in the *S. barungensis* pollen, suggesting that it may represent a range of possible taxa, including Typhaceae/Sparganiaceae, Potamogetonaceae and *Ruppia* (Gandolfo et al. 2009). *Ruppia* pollen does not preserve well in sediments or transport easily, its presence in sediments is generally taken to indicate a local source (Ashworth and Markgraf 1989). Potamogetonaceae pollen is listed as present in New Zealand from the early Miocene onwards (Mildenhall 1980; Conran et al. 2015b), but it is unclear on what these pre-Quaternary records were based.

Machin (1971) suggested that there were similarities of the fossil palynomorph *Aglaoreidia cyclops* Erdtman to Ruppiaceae and Potamogetonaceae, proposing a possible relationship with the extinct fossil fruit genus *Limnocarpus* Reid emend Reid and Chandler. Collinson (1983) supported this, noting that *A. cyclops* pollen was morphologically intermediate between *Ruppia* and *Potamogeton* and occurs with pollen of other aquatic macrophytes. However, although *A. cyclops* occurs in some Western Australian Upper Eocene lignites (Sanchez Botero et al. 2013), it is absent from Australian and New Zealand Cenozoic sites where pollens have been examined previously (Hill 1994 and papers therein; Raine et al. 2011).

### *1.2.6 'Seagrass' Fossils*

The fossil evidence on seagrasses was reviewed by den Hartog (1970) and Larkum and den Hartog (1989) and more recently, as part of the reviews of Alismatales listed above. Seagrass macrofossils are rare, but leaves with cuticular impressions from the Late Cretaceous of Belgium were placed into the extinct genus *Thalassotaenia* R.W. Ham and van Konijnenb and allied to the Cymodoceaceae–Zosteraceae–Posidoniaceae clade (van der Ham et al. 2007). Fossil seagrasses have been described from as early as the Cretaceous, where the genera *Archaeozostera*, *Thalassocharis* and *Thalassotaenia* were present (Koriba and Miki 1931, 1958; Oishi 1931; Voigt and Domke 1955; van der Ham et al. 2007). Brongniart (1828, 1849) described fossil seagrasses from locations of Eocene age in the Paris Basin. Eocene *Cymodocea* and *Caulinites* species were described as seagrasses by Watelet (1866), Bureau (1886) and Laurent and Laurent (1926), although Fritel (1909, 1914) reassigned the *Caulinites* specimens to *Cymodocea* (*Posidonia*) *parisiensis* (Brongt.) Fritel and *Cymodocea* (*Cymodoceites*) *nodosus* (Brongt.) Fritel. Other fossil Potamogetonaceae-like remains attributed to seagrasses by Ascherson and Graebner (1907) were fragmentary and difficult to determine precise affinities.

Dixon (1972), Randazzo and Saroop (1976) and Lumbert et al. (1984) all reported fossils of extant seagrass genera in the Cymodoceaceae (*Cymodocea* K.D. Koenig, *Halodule* Endl., aff. *Ruppia* and *Thalassodendron* Hartog) and Hydrocharitaceae (*Thalassia* Banks ex K.D. Koenig) from the Eocene Avon Park Formation in Florida, although there is some uncertainly of their affinities (Iles et al. 2015). A further Hydrocharitaceae fossil (*Thalassites parkavonenses* Benzecry and Brack-Hanes) was described from the site by Benzecry and Brack-Hanes (2008), indicating that the area had at least seven species of seagrass at the time of deposition (see also Ivany et al. 1990).

The early Eocene Monte Bolca Pesciara limestone contains diverse marine monocots (Wilde et al. 2014; Fig. 1.1), including well-preserved rhizomes, ligulate leaves displaying possible tannin cells and inflorescences, suggesting the presence of several members of the Cymodaceae–Zosteraceae–Posidoniaceae complex. There are also possible Ruppiaceae-like fossil impressions and Najadaceae-like shoots with apparently whorled clusters of finely-toothed leaves. Gregor (1991) described two these fossils as Posidoniaceae: one with reproductive structures as *Posidocea frickhingeri* Gregor and the second (*Posidonia parisiensis* Gregor) from the nearby San Floriano deposit, based on rhizomes; however, the inflorescence structure of *Posidocea* differs considerably from modern *Posidonia* K.D. Koenig

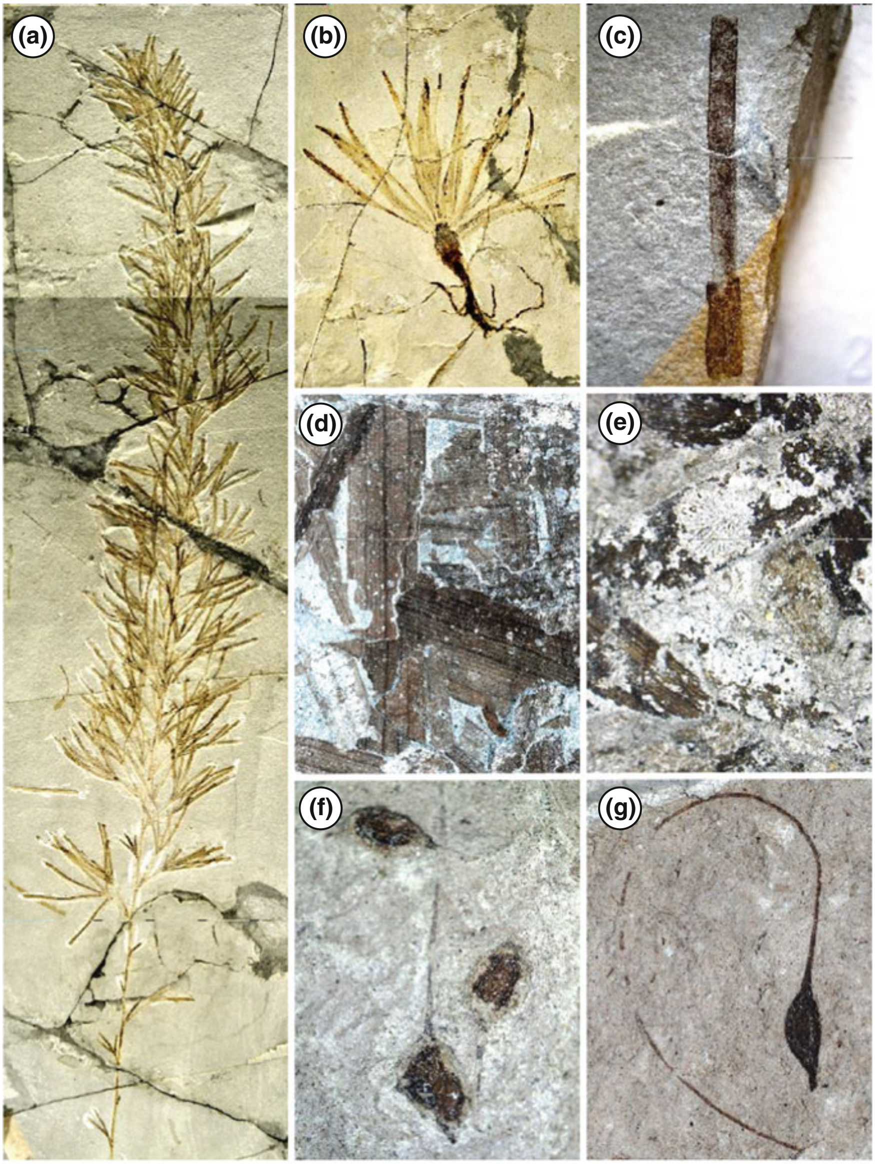

**Fig. 1.1** **a**–**c** Examples of seagrass fossils from the Eocene Pesciaria di Bolca site (Italy); **a** *Halochloris cymodoceoides*; **b** *H. veronensis*; **c** Ligulate *Zostera*–like leaf; **d**, **e** Miocene–Pliocene-aged *Enhalus*-like revolute-margined seagrass leaves from New Zealand; **d** Late Miocene leaves from near Amberley, South Island; **e** Pliocene leaves with attached crustose algae from Weymouth near Auckland, North Island; **f**, **g** *Ruppia*-like long-pedicellate fruits from New Zealand; **f** Miocene-aged endocarps from palaeo-lake Manuherikia, South Island; **g** Pliocene-aged endocarp from Ormond, North Island

species and its affinities require further investigation. Nine of the other seagrass-like monocots at Bolca were described as species of *Halochloris* Unger by Massalongo (1859) and Massalongo and Lotze (1859). However, the affinities of most of these fossils are very uncertain and many of them were described previously by Massalongo (1850, 1851, 1852, 1856) variously as species of algae (e.g. *Condrites* Sternb. or *Zonarites* Sternb.) and/or aquatic monocots such as *Ruppia* (Ruppiaceae) or *Mariminna* Unger (Najadaceae?). There is also the nomenclatural issue that the name *Halochloris* P.J.L. Dangeard (1965), although a later homonym of *Halochloris* Unger (1847), is used for a currently recognised green algal genus in the Chlorococcaceae (Guiry 2014). More work is therefore needed to sort out the taxonomy and nomenclature of the seagrass-like monocotyledons at Bolca and their diversity and palaeoenvironment are the subject of ongoing study.

In New Zealand, there are currently no published pre-Holocene seagrass fossils (Conran et al. 2015a, b). However, a recent determination that there are late Miocene–Pliocene seagrass fossils from South Island with apparently revolute leaf margins, suggesting affinities to the present day tropical to subtropical Hydrocharitaceae genus *Enhalus*, although pollen at the site indicates that the palaeoclimate at the time was at best warm temperate (Conran et al. unpublished data). The identity and affinities of these fossils are the subject of ongoing research. There are also characteristic, fossilised seagrass limpet shells of the family Lottiidae (Mollusca: Patellogastropoda) present at an Oligocene estuary and palaeoshoreline at Cosy Dell in Southland (Lee et al. 2014; Conran et al. 2014). Based on the biology of living relatives which are obligate grazers on seagrass leaves (Nakano and Ozawa 2007) and their use to infer former seagrass meadows in Onepoto Lagoon, New Zealand 8.1 Ka (Hayward et al. 2002), these Oligocene limpets were regarded as proxy evidence for the presence of Zosteraceae growing in shallow inshore waters at the site (Conran et al. 2014).

Because of the rarity of seagrass fossils, presumed obligately- or strongly-associated proxies are often used to infer their presence in the fossil record, with Brasier (1975) and Eva (1980) using foraminifera to suggest that seagrasses were distributed widely during the Late Cretaceous of the Caribbean. Various groups of molluscs, crustacea, foraminifera and some vertebrates, such as sirenians and certain seahorses are often associated with seagrasses (e.g. Ivany et al. 1990; Teske and Beheregaray 2009; Battley et al. 2011; Unabia et al. 2011) and their abundance as fossils has been used as a proxy for inferring fossil seagrass ecosystems in the absence of actual plant remains (e.g. Domning 2001; Leonard-Pingel 2005; Buchan 2006; Reuter et al. 2011; Velez-Juarbe 2014). We discuss several of the more commonly applied methods of inferring the presence of seagrass ecosystems; however, there are limitations to the 'proxy equals presence' approach and some caution is advised (Reich et al. 2015).

### *1.2.7 Foraminiferan Evidence*

Wright and Murray (1972) first presented evidence for seagrasses in ancient deposits. This work was continued by Brasier in the Caribbean (see Brasier 1975) and has been continued in the recent studies of Parker and Gischler (2015).

Brasier showed that some shallow tropical foaminiferans have the same geographical distribution as tropical seagrass beds. Some foraminiferans are collocated with characteristic seagrass species, such as *Peneroplis plaanuatus* with *Cymodocea* spp. in the Carribeean and *Amphisorus hemprichii* and *Sorites marginalis* with *Thalasssia testudinum* (Brasier 1975). However, these same foraminifera can be associated with certain algae as well, so the correlation needs to be taken with caution (Heck and McCoy 1979; Eva 1980). Furthermore there is little evidence that similar associations occur in temperate communities.

Despite these caveats, the predictive value of foraminiferan deposts is high, from the Palaeocene–Eocene onwards. Thus Brasier (1975) put forward a coevolutionary scheme based on foraminiferal remains, seagrass fossils and present distributions. Nevertehless, Eva challenged the view that seagrasses did not arrive in the Caribbean until the Oligocene. He suggested that an extensive seagrass population existed in the Eocene, a view supported by the finding of the Eocene seagrass species at Avon Park, Florida (Lumbert et al. 1984; Benzecry and Brack-Hanes 2008). Moreover Wright and Murray (1972) also inferred from foraminiferal remains that seagrass beds (*Cymodocea* and *Posidonia*) were widespread in the middle and late Eocene deposits of the English Channel, supported by the presence of fossil seagrasses in the Paris Basin.

### *1.2.8 Other Associative Evidence*

There is evidence from other proxies apart from those that have been used to assess previous seagrass cover. This work has been summarised recently (Reich et al. 2015) and such studies are based in the main on the presence of gastropods, crustose coralline algae and fossil Sirenia.

#### 1.2.8.1 Gastropods

Reich (2014) looked at the gastropod distribution in seagrass-vegetated and unvegetated sand flats in the Bahamas. Multivariate analysis clearly demonstrated that species composition of gastropods was a tool for distinguishing seagrass areas from unvegetated areas. Feeding guild composition based on species richness also differed between the two states. The results suggested that gastropod assemblages are a useful proxy for seagrass meadows in the fossil record. These preliminary results now need to be put to the test in a real fossil situation and Harzhauser (2014) contemporaneously looked at gastropods associated with putative seagrasses in Miocene deposits of SW India (Kerala).

#### 1.2.8.2 Crustose Coralline Algae

Crustose coralline algae (CCA) are a characteristic feature of seagrass structures that grow in the water column, particularly the flat surface of leaves (e.g. Fig. 1.1e). They are an early coloniser and in turn are colonised by other algal epiphytes. As crustose coralline algae also colonise other surfaces that remain exposed it may be difficult to correlate their presence with seagrass beds. However, Beavington-Penney et al. (2004) have shown that CCA colonise seagrass leaf blades and leave behind a characteristic “hooked” form. These “hooked forms have been recognised in modern seagrass deposits and in fossil remains from the Eocene of Oman. Thus this line of research holds out promise for the future.

#### 1.2.8.3 Sirenia

Fossil Sirenia also provide insights into the evolutionary ecology of seagrasses on which sirenians are known to be specialist grazers (Domning 1981, 2001). Sirenia (manatees and dugongs) are linked strongly to an association with marine plants and in particular seagrass beds, having co-evolved, as far as current evidence goes, with seagrasses. Indeed the evolution of Sirenia seems to have depended on the presence of seagrasses (Fitzgerald et al. 2013), as unlike herbivorous marine turtles which feed on seagrass leaves but also eat algae, Sirenia feed on both leaves and in some cases the rhizomes, which are rich in carbohydrate reserves (Marsh et al. 2011; this volume, Chap. 19).

In his seminal review Domning (2001), describes an evolutionary hypothesis that links the fossil record of sirenians, particularly in the tropical Western Atlantic Ocean to a dramatic change in community composition of seagrasses. Indeed, Domning links coevolution of seagrasses and Sirenia throughout the Eocene, through the Palaeocene and to the present time by associating the decline of species diversity in both groups. He suggested that up to 2–3 Ma, around the time of the closure of the Panamanian Isthmus, seagrass ecosystems were largely herbivore-based; however, after that they became detrital-based, which was associated with a great decline in sirenian communities. Domning and coworkers have made many observations in the Caribbean and West Atlantic region describing fossil sirenians and their palaeoecology (e.g. Velez-Juarbe 2014; Springer et al. 2015). Velez-Juarve (2014) has also discussed possible reasons for the late arrival of sirenians and seagrasses in Australia and South America. Fitzgerald et al. (2013) have presented evidence of a fossil sirenian from New Guinea, which at >11.8 Ma, is the oldest known sirenian from the Indo-Pacific.

Clearly these fragmentary and exiguous pieces of evidence from such diverse methods provide challenging opportunities to gain greater insights into the evolutionary ecology of seagrasses.

## 1.3 Biogeography of Seagrasses

The study of biogeography represents the synthesis of knowledge from disciplines that include understanding species distribution in space and through time. In practice, the models that biogeographic studies test attempt to describe the causal nature of extant and palaeo distributions of species following concepts such as: dispersal-vicariance; centre of origin; track analysis and many others (Crisci et al. 2003). An important additional component to understanding biogeography can be the inclusion of information on the evolutionary origins of species and their relatives. This has led to the growth of a sub-discipline called phylogeography (Avise 2000) that seeks to incorporate phylogenetic information into hypotheses that explain the geographic distributions of species.

Discussions of seagrass biogeography have, in the past, evaluated the fundamental distribution of species as being largely the result of isolation over time (vicariance) as a result of continental drift (den Hartog 1970; Larkum and den Hartog 1989). This concept has been supported by the determination that there is a long evolutionary history of seagrasses (see above). However, newer studies have determined that seagrasses have evolved in four independent lineages (Les et al. 1997) and that these lineages have different evolutionary trajectories (Waycott et al. 2006). There is also the potential that distributions are due to adaptation limits of species such as temperature tolerance limits.

One such hypothesis is that the ‘centre of origin’ of a species is the region with the highest number of species of a given taxon from which it has spread by radiation to other regions. Thus for seagrasses, if treated as a single lineage, the fact that the region around Malesia (Indonesia, Borneo and New Guinea) has the greatest concentration of seagrass species today might suggest this as the centre of origin of seagrasses in the region (Mukai 1993; Short et al. 2007). However, if the age of seagrasses, their varied evolutionary patterns and geological history are taken into account, this simple hypothesis seems less acceptable and other hypotheses become attractive. For example, a vicariance hypothesis postulates that the current distribution of a region was initially much more widespread and has been constrained by special radiations, plate tectonic movements and local speciation and extinctions. McCoy and Heck (1976) compared the current distribution of corals, seagrasses and mangroves in the Indo-Pacific. They showed that generally these three disparate ecosystems have similar distribution patterns, with the highest number of species occurring in the Malesian region, although smaller areas of increased species number occur on the East African coast. They concluded that a vicariance hypothesis fitted the facts best, based on the widespread occurrence of all groups in the Tethyan seas of the Cretaceous. The vicariance hypothesis has merit in focusing attention on a number of distribution mechanisms, including plate tectonics and turning attention away from just the present biogeography. However, too strong an adherence to the vicariance hypothesis may itself become dogmatic (Heck and McCoy 1979). Also it should be borne in mind that stochastic events such as the postulated contemporaneous decline of sirenians and seagrasses, due to co-evolutionary destructive interactions (see above) may provide special explanations; in this case for the combined losses of sirenian and seagrass stocks around the world in previous times (before 2 million years ago).

The advent of molecular clock testing of biogeographic models of species distributions on a global scale has been successfully applied to seagrasses and other aquatic plants by Les et al. (2003). These authors evaluate the very widespread distribution of many aquatic plant groups, species and genera and essentially test that these ranges have the potential to represent either long-term isolation at the global scale, or long distance dispersal. Among the species pairs assessed, Les et al. (2003) tested the divergence times between *Thalassia* species (from Australia and North America), *Posidonia* species (from the Mediterranean and Australia) and *Zostera* species (from Australia, Europe and North America). In all cases, the disjunction could have been the result of long-term vicariant speciation associated with continental drift and isolation. In all cases, the molecular clock estimate for the divergence time was significantly lower than would have been expected under a continental drift, isolation, vicariance model (Les et al. 2003; see Chap. 5 for additional discussion). Finally, other models of speciation may reflect more ecologically based divergence of seagrasses into tropical and temperate genera through adaptation and selection.; but in general the apparent matching of seagrasses, corals and mangrove distributions in the tropics can be upheld (McCoy and Heck 1976).

### 1.3.1 The Present Distribution of Seagrasses

There are currently 11 genera of seagrasses, excluding the genera *Ruppia* and *Lepilaena* and ca. 65 species (Chaps. 4, 5 and Appendix). This number of taxonomic groups adopts the recent view that the genus *Heterozostera* should be merged with *Zostera* (Jacobs et al. 2006) (but see the Appendix). A recent review of geographic regions of seagrasses by Short et al. (2007) provides a broad bioregional classification that allows clustering of species present in thermal and oceanic regions (Fig. 1.2). However the biogeography of seagrasses of the world was well established before 1940 (Ascherson 1876, 1906; Ostenfeld 1915, 1927a, b; Setchell 1920, 1935). The addition of the magisterial opus of den Hartog (1970) generated a significantly enhanced view of the world's seagrass flora. Since that time over 10 seagrass species have been added around the world bringing the total to ca. 65 (see Chap. 5 and Appendix). The majority of early workers set their conclusions on the current geographical limits of species; in particular Setchell (1915, 1920) made the useful contribution of considering the influence of water temperature on distribution patterns. He made the important distinction of defining species distribution

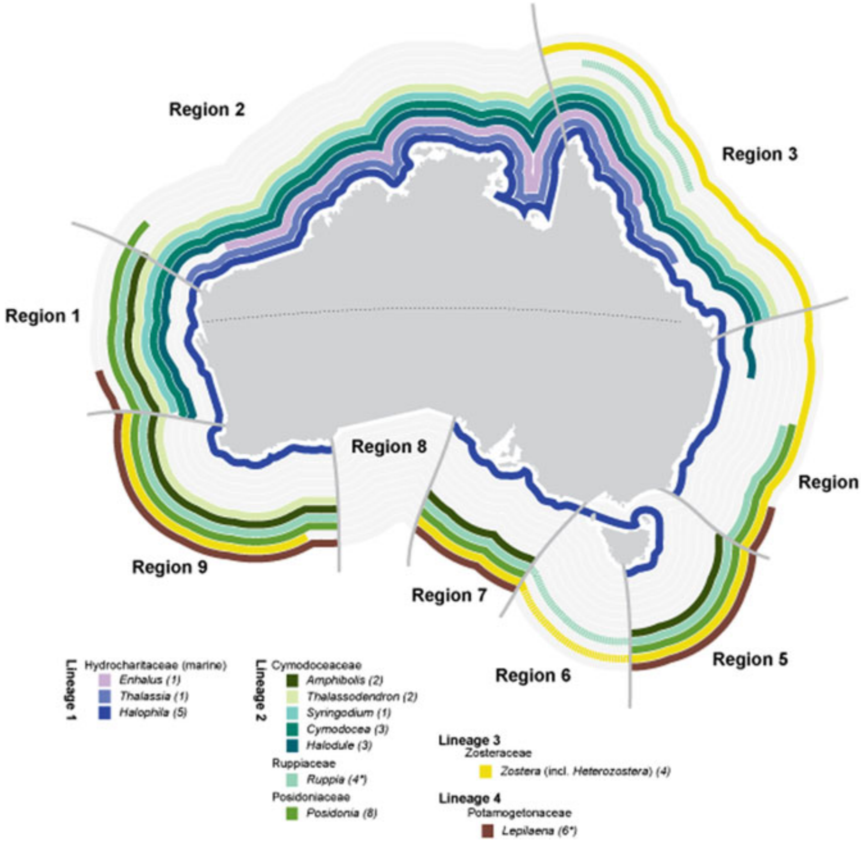

**Fig. 1.2** Australian extent of each seagrass genus indicated by solid, concentric, lines parallel to the coast. Dashed lines indicate areas where members of two genera, *Ruppia* and *Lepilaena* occur but there is uncertainty as to any marine occurrences in the zone indicated. Regions, bounded by grey lines perpendicular to the coast, are numbered arbitrarily and clockwise starting with the major tropical/temperate overlap zone on the West coast. The dashed line across the continent represents the Tropic of Capricorn. Faint grey lines are to provide reference for the zones where genera do not occur. The number of species in each genus is indicated in parentheses next to the genus name in the legend, *indicates the number of species includes potentially non-marine taxa requiring review. Colours are clustered according to lineage, in particular (and in order), 'purple' for the marine Hydrocharitaceae and 'green' for the Cymodoceaceae/Posidoniaceae/Ruppiaceae group, 'yellow' for Zosteraceae and brown for Potamogetonaceae

according to the mean water temperature of the warmest month (tropical 25 °C; subtropical, 20 °C; temperate, 15 °C; cold temperate, 10 °C) (Setchell 1915, 1920).

The evolutionary stability and fitness of seagrasses are topics of importance but which have been only tentatively explored until recently (e.g. Williams 1995; Reusch 2001a, b; Reynolds et al. 2012). In terms of species persistence through geological time, seagrasses may be viewed as highly successful. The reproductive strategies of seagrasses enable their survival; the advent of modern molecular genetic and analytical techniques has enabled an improved understanding of influences on their survival (e.g. Waycott 1995; Reusch 2001a, b; Waycott et al. 2006; van Dijk et al. 2009; Kendrick et al. 2012; McMahon et al. 2014). Further exploration of these factors in seagrass adaptation are presented throughout this book (see Chaps. 5, 6, 8, 10, 6, 12, 15, 21, and 22).

### *1.3.2 Seagrass Distribution and Biogeographical Regions*

There have been six global seagrass bioregions established that capture the nature and scale of seagrass communities, and their associated floras (Short et al. 2007). Seagrass genera are typically affiliated with tropical or temperate environments (Short et al. 2007; Waycott et al. 2004, 2014). Tropical seagrasses have a greater proportion of taxa within them, seven of the 11 current genera of seagrasses have a tropical distribution: *Halodule, Cymodocea, Syringodium, Thalassodendron, Enhalus, Thalassia* and *Halophila*. The other four are confined to temperate waters: *Zostera, Phyllospadix, Posidonia* and *Amphibolis*. In addition, there are two genera that are sometimes not discussed when considering as seagrass biogeography, *Ruppia* and *Lepilaena*; however, they can co-occur with seagrass species, in marine habitats so are included here (Waycott et al. 2004, 2014). These are both typically temperate groups although *Ruppia* has a particularly widespread distribution globally and is found in tropical latitudes although more commonly and with higher diversity in temperate regions.

There is an overlap of tropical and temperate groups in the seagrass floras on the West Australian coast (Fig. 1.2, Region 1). This overlap is associated with north/south flowing currents of warm or cold water, along the West coast of Australia, predominated by the south flowing Leeuwin current. The Leeuwin current provides warmer waters much further to the south than would otherwise occur facilitating the broader distribution of tropical seagrasses (Walker 1991). In fact, this region is unusual in a global context as most of the western coasts of continents have depauperate seagrass floras due to poor habitat including colder waters from deep ocean upwellings (den Hartog 1970; Green and Short 2003). In contrast, on the east coast of Australia, there is a distinct region depauperate of seagrass species south of the major north-eastern facing bays of Queensland, and the presence of the widespread temperate species that occur in sheltered bays along the NSW coastline (Fig. 1.2, Region 4). Interestingly this contrasts with a region of high diversity, and overlapping temperate and tropical floras terrestrially in this same region (Burbidge 1960; Ebach et al. 2015). The western coast of Tasmania, and the ocean-facing coast of Victoria have only a few seagrasses: only those that occur in estuarine systems, i.e. *Zostera, Halophila* and *Ruppia* species (Fig. 1.2, Region 6). The Great Australian Bight is distinctly lacking in a seagrass flora although occasional records, most likely drift, have been described (Kirkman 1997). This depauperate seagrass flora is likely due to the fact that this region is exposed to very high-energy, deep swells from the Southern Ocean and the fine silica grained sands that are highly mobile (Carruthers et al. 2007). Indeed the significant limitation to the existence of seagrasses in temperate Australian ecosystems is where exposure to high energy waves/oceanic conditions is at its extreme.

There are variable broad scales of distribution geographically among seagrass species within genera. In Australia, for example, *Halophila ovalis* stretches from northern Queensland to southern New South Wales on the East coast, and to the lower corner on the south-west coast, where in both regions it is replaced by *Halophila australis*. *H. australis*[1] has a restricted, temperate Australian endemic distribution from the South West of Western Australia to southern Tasmania and a small section of the east coast of Australia. *Halophila ovalis* is highly eurythermic in general and in other parts of the world it is found in Japan and across the Indian Ocean as far north as the Suez canal (e.g. Waycott et al. 2004). It is worth noting that in general for *Halophila* species, most are tropical and it is only in the case of *H. australis*, in Australia that a purely temperate species has evolved. There are at least two tropical genera that have produced species that are now restricted to sub-tropical or warm temperate waters, both in Australia, viz. *Cymodocea nodosa* (found in the Mediterranean Sea and the West coast of Africa) and *Thalassodendron pachyrhizum* (found in Western Australia). On the other hand at least four species of the temperate genus *Zostera* (subgenus *Zosterella*) extend, in different regions, into tropical/sub-tropical waters: viz. *Z. capensis, Z. muelleri, Z. japonica* and *Z. noltii*.

The tropical seagrasses are not distributed homogeneously, but are concentrated into two large, but widely separated areas globally. The Indo-West Pacific contains all seven of the tropical genera. *Thalassodendron* and *Enhalus* are endemic and *Cymodocea* is largely confined to that area (i.e. *C. nodosa*). Four of these genera occur in the Caribbean area as well as the Indo-West Pacific: viz. *Halodule*, *Syringodium, Thalassia* and *Halophila* and two of these (*Halodule* and *Halophila*) also occur on the central west Pacific coast of South America. However, it should be pointed out that this region is little explored and highly disturbed by riverine inputs (Creed et al. 2003). The three species that have been reported there: viz. *Halodule wrightii, H. beaudettei* and *H. baillonis*, also have a wide distribution in the Caribbean and likely migrated to the West when the two Americas were still separated (Creed et al. 2003). *H. wrightii* has also been reported as far North as the Gulf of California (McMillan and Phillips 1979). The tropical Atlantic does not have any endemic genera, but its species are different from those of the Indo-West Pacific, suggesting ancient speciation in these genera. The exceptions here are *Halophila decipiens*, which is a very widely distributed pan-tropical species (see

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[1] Current distributions of species of seagrasses in Australia are inferred from data available on Australia's Virtual Herbarium (avh.ala.org.au), published accounts including Green and Short (2003), Carruthers et al. (2002, 2007a, b), IUCN Redlist distributions (iucnredlist.org see Short et al. 2011), regional mapping and field guide resources (Carter et al. 2016; Waycott et al. 2004, 2014; seagrasswatch.org).

McMahon and Waycott (2009) for extension into Kenya) and *Halodule wrightii,* which has a centre in the Caribbean, but also may occur on the coast of East Africa.

The high species diversity in the Indo-West Pacific means that there can be up to 12 seagrass species in any one location (Green and Short 2003) and 35% (17) of the total number of seagrass species occur here. Most of these species have a wide distribution, but six have a more restricted range. These are *Halodule pinifolia, Thalassodendron ciliatum, Halophila stipulacea, H. beccarii, H. spinulosa, H. tricostata*, *H. capricorni* and *H. sulawesi* (and now *H. nipponica*, *H. major;* Uchimura et al. 2008). This pattern was the basis for the Malaysian and East African seagrass groups that were distinguished originally by Ostenfeld (1915), but with more complete records these geographic groupings can no longer be maintained. *Thalassodendron ciliatum* has a disjunct distribution (East African coast, Eastern Indonesia, Northern Australia, New Guinea, the Philippines and rarely in the Solomon Islands) and *Thalassodendron leptocaule* has recently been distinguished from *Thalassodendron ciliatum* as a separate species on the East African coast (Duarte et al. 2012). *Halophila stipulacea* occurs only in the Western part of the Indian Ocean (although since the opening of the Suez Canal it has spread extensively in the Mediterranean, den Hartog 1970) and thus it may well have suffered extinctions in recent times. More recently, *H. stipulacea* has been found in the Caribbean and is now recognised as having the capacity to disperse globally (Willette and Ambrose 2009).

In the Atlantic there are only four seagrass genera and nine species and these are less homogenously spread in comparison to the Indo-West Pacific. The main region of biosiversity is in the Caribbean, where three genera are represented by one species each and *Halophila* by four species, including *H. johnsonii* (Eisenman and MacMillan, 1980) whose taxonomic status remains controversial (Waycott et al. 2002; Short et al. 2010). The Atlantic coastal areas South of the Equator have a very depauperate flora. The West coast of Africa has only one species (*Cymodocea nodosa*) and the coast of Brazil has four species from only two genera (*Halophila* and *Halodule*). It is possible to hypothesise that the tropical species of seagrass had a more pan-tropical distribution before the upheaval of the Central American Isthmus in the Miocene. After this it is possible that the species diverged to give rise to the so-called twin species, which have only slight morphological differences but are widely separated from each other. The three sets of twin species proposed by den Hartog (1970) are:

| Indo West Pacific | Tropical Atlantic |
|---|---|
| *Halodule uninervis* | *Halodule wrightii (syn. beaudettei)* |
| *Syringodium isoetifolium* | *Syringodium filiforme* |
| *Thalassia hemprichii* | *Thalassia testudinum* |

These twin species are most likely the result of a broader geographically distributed progenitor that became subsequently isolated and have diverged through isolation (i.e. vicariance). Across these major biogeographic regions there has also been loss of species (especially as a result of the probable sirenian/seagrass dieback (see above) in the tropical Atlantic region in particular, which in the Eocene appeared to have *Thalassodendron* and *Cymodocea* present based on high quality fossils (Ivany et al. 1990).

The Australian region shows a great diversity of species and likely represents the greatest endemism of any region in the world and is discussed extensively elsewherein this book (see Chaps. 2–6). The distribution of seagrass genera around Australia is shown in Fig. 1.2. Very broadly, a distinction can be made between the tropic/subtropical regions and the southern temperate zone, with a rather distinct transition point at about 25°S on the West coast and 30°S on the East coast. The difference between latitude cutoffs on the West and East coast, as well as the exceptions of *Zostera muelleri* and several species on the West coast (Fig. 1.2), has not been successfully explained. A reasonable working hypothesis is that the edges of the ranges of these species are dispersal limited and relate to the overall movement ecology of each species (i.e. Kendrick et al. 2012; McMahon et al. 2014).

The subtropical/tropical seagrasses of Australia belong to the members of two lineages, the Cymodoceaceae and Hydrocharitaceae, representing an Indo-Pacific group (Fig. 1.2). Two tropical genera have species endemic to Western Australia: *Cymodocea angustata* and *Thalassodendron pachyrhizum*. The genus *Thalassodendron* is particularly interesting because it has a disjunct distribution in the Indo-Pacific, one a tropical species, *T. ciliatum* occurring right around from Queensland and the northern Territory to the far North of Western Australia, with the endemic *T. pachyrhizum* occurring only south of 25°S on the Western Australian coast. The genus *Thalassodendron* is known to have had a much wider distribution in Eocene times (Lumbert et al. 1984) and *T. pachyrhizum* may well be a relict of a wider, former distribution. The situation for *Cymodocea angustata* (see above) may be a similar.

The temperate seagrasses of Australia divide into several, broad groups:

1. Restricted to the West coast and not reaching the Great Australian Bight; viz. *Cymodocea angustata*, belonging to a genus with tropical affinities.
2. Restricted to the West coast, each side of the Great Australian Bight, South Australia, Vicotria and Tasmania viz. *Amphibolis antarctica* and *A. griffithii*, the *Posidonia* complex, apart from *P. australis*, *Thalassodendron pachyrhizum* and *Zostera muelleri* (den Hartog 1970; Cambridge and Kuo 1979; Kuo and Cambridge 1984).
3. Present in all temperate regions, including the East coast; viz. *Zostera tasmanica*, *Z. muelleri* (which also extends into Queensland), *Posidonia australis*.
4. Restricted distribution across southern temperate Australia—South Western Australia, Victoria, Tasmania and parts of southern NSW; viz. *Halophila australis* (Waycott et al. 2014).

It should be noted that prior to the merger of *Zostera capricorni*, *Z. muelleri*, *Z. mucronata* and *Z. novazelandica*, two previous species would have had restricted distributions: *Z. capricorni* from the East coast to Victoria and *Z. mucronata* to group (ii) (den Hartog 1970). Now any taxonomic differentiation must be ascribed to local sub-species which follow a general trend of *Z. muelleri* subsp. *capricornii* in the tropics subsp. *novazelandica* in New Zealand and subsp. *mucronata* in western and southern Australia. The general distributions described above strongly suggest a general radiation from West to East, with *Zostera muelleri* and *Halophila decipiens* being the exceptions. Another exception is *Halophila ovalis*, which occurs off all coasts around Australia, with the exception of the Great Australian Bight, where it is replaced by *H. australis* (den Hartog 1970).

The zoological provinces in southern Australia were set out by Knox (1963), who described West Australian, Flindersian and Maugean Provinces. It is possible to see correlations with seagrass distributions in these regions. Sea level changes during the Pleistocene and Holocene Epochs help to explain the distributions in terms of a long-term land bridge between Tasmania and the mainland during this period. For example, the absence of *Posidonia australis* in most of Victoria despite its presence in New South Wales on the one hand and in Tasmania and South Australia on the other, may be the result of recent land emersion and unsuitable sites in Victoria. The slow colonisation rates in this region (Larkum and West, 1983; Meehan and West 2000) are consistent with this view and again relate to the movement ecology of these species (McMahon et al. 2014). Those species present in Port Phillip Bay and Western Port (*Amphibolis antarctica*, *Zostera tasmanica* and *Z. muelleri*) are all fast growing and able to colonise unstable habitats.

Global climate change is expected to affect the future distribution of seagrass species in Australia. Discussion of predicted changes is given in Chap. 21.

## 1.4 New Zealand, Our Close Neighbour

In striking contrast to Australia, New Zealand has only one species of seagrass, *Zostera muelleri*. Formerly two species were recognised, *Z. capricorni* and *Z. novazelandica* (den Hartog 1970); however, the latter is now recognised as a sub-species (Jacobs et al. 2006). Thus, despite having separated from Antarctica at about the same time as Australia (~80 Ma) and just at the time that many seagrass species originated (the Late Cretaceous), the seagrass floras are strikingly different. If, as stated for temperate Australia the majority of species migrated from Western Australia and those that came down the east coast were late arrivals, this may provide some explanation for the paucity of species in New Zealand. Together with the fact that New Zealand has undergone considerable climate change and tectonic effects and significant land area reduction on at least one occasion, over the same period that Australia has been fairly stable, are powerful reasons that seem to explain the differences (see Lee et al. 2001). A recent study of the genetic connectivity between Australian and New Zealand populations of *Zostera muelleri* (Ticli 2014) has demonstrated that the New Zealand populations likely represent a long distance dispersal event from the East coast of Australia.

## 1.5 Conclusions

Recent analysis of the fossil record have identified good seagrass fossils, and these encourage the view that seagrasses have often had a wider distribution in the past compared with today. They also suggest that the discovery of new fossil sites should be encouraged and that these will produce important valuable information.

In general the biogeography of seagrasses suggests that these organisms evolved successfully in Tethys seas of the Late Cretaceous. However, the modern division into two groups, temperate and tropical tends to suggest that at some point an ecological separation occurred, possibly occurring in both the Northern and Southern Hemispheres.

The large number of temperate species in southern Australia and the endemism shown by the genus *Posidonia* are interesting features of the seagrass flora of Australia. The use of genetic techniques over the last decade (Chaps. 5, 6 and 8) has helped to explain this phenomenon to a certain extent and the laws of seagrass viability in general, but we can expect a much bigger picture to emerge in the future.

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# Chapter 2
# Biogeography of Australian Seagrasses: NSW, Victoria, Tasmania and Temperate Queensland

**Peter I. Macreadie, Brooke Sullivan, Suzanna M. Evans and Timothy M. Smith**

**Abstract** This chapter presents an introduction to the biogeography of south-eastern Australian seagrasses, explaining the distribution and basic ecology of the 22 species that inhabit this 10,000 km stretch of coastline, from the northern limit of Queensland's temperate zone through to Tasmania. The chapter draws on 25 years of new information (peer-reviewed literature, books, personal communications, etc.) that has been generated since the previous biogeography chapter of its kind was written by Larkum et al. (Biology of Seagrasses—a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, The Netherlands, 1989). The influence of local (e.g. geomorphic environment) and large-scale (e.g. temperature) factors on the distribution of species are discussed. Also, we present up-to-date information on the status (declining, increasing, or no change) of each species from a conservation point of view on a state-by-state basis. Not surprisingly, many species are reported to have declined for a variety of reasons, including: flood events, boat moorings, and coastal development (e.g. dredging). Fortunately, there are also reports of recovery. Thanks to developments in genetic sequencing we have been able to present new data on genetic connectivity, gene flow, and source-sink populations for a handful of species. In the coming years we expect and hope that improvements in remote sensing technology will allow for more accurate, more frequent, and higher resolution mapping of seagrasses along this stretch of coast.

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## 2.1 Introduction

This chapter describes the biogeography of southeastern Australian seagrasses; a ~10,000 km stretch of coastline (Fig. 2.1) spanning the states of New South Wales (NSW), Victoria (VIC), Tasmania (TAS), and temperate Queensland (QLD). In total, seagrasses within the region considered cover an area of approximately 4,213 km$^2$ (Rees 1993; excluding 12,000 km$^2$ of deepwater seagrass in temperate QLD, Blake and Ball 2001a, b; McKenzie et al. 2010), with the majority (80%) in QLD. The majority of seagrass is located within intertidal and shallow subtidal estuarine habitats, which includes many sub-habitats, such as lagoons, tidal creeks, and embayments. The remainder can be found in deepwater environments, although relatively little is known about deepwater seagrasses in this region. The number of species in southeastern Australia is approximately 22, although there is ongoing

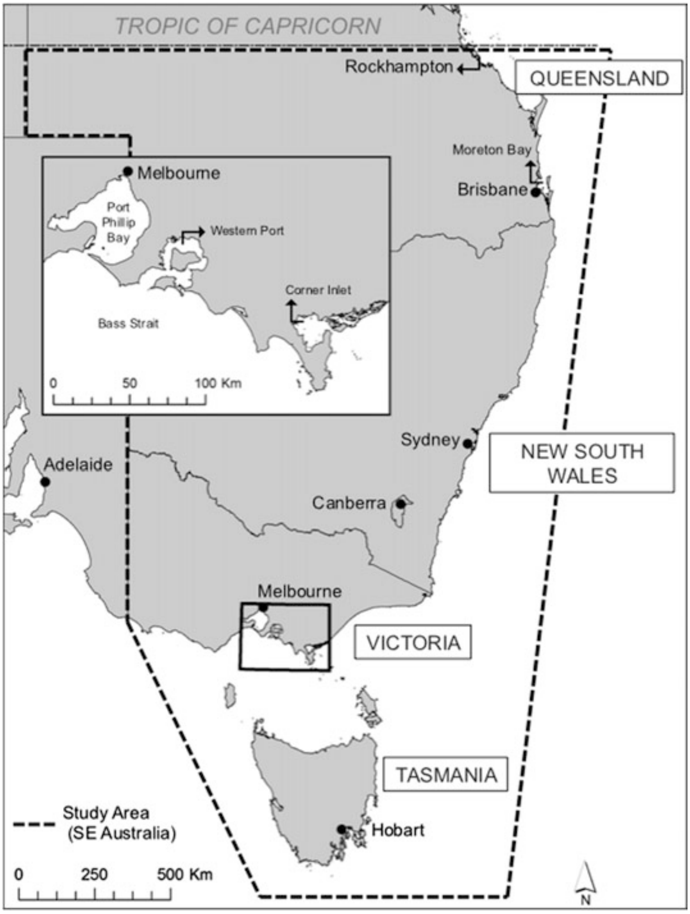

**Fig. 2.1** Region of coast and key sites covered in this chapter

debate about what constitutes a seagrass species in Australia, including how some species are classified and grouped.

The main difference between this biogeography chapter and the one previously published by Larkum et al. (1989) is that this updated version has benefited from technological improvements that have occurred over the past >25 years, that have allowed seagrass for improved identification of seagrass species (via genomics) and improved mapping of seagrass distribution (remote sensing). We have drawn on a broad variety of information sources in preparing this chapter, including: peer-reviewed literature, books, reports, herbarium records, personal communications from fellow scientists and resource managers, as well as our own knowledge. Because the mapping of southeast Australia's seagrass has been undertaken in a piecemeal approach (i.e. by state agencies, local councils, individual researchers, and fisheries) as opposed to a coordinated national effort, there is no central database containing seagrass maps. Furthermore, much of the information we have obtained isn't in the public domain or easily accessed. A recommendation for the future would be to collate and centralise information (e.g. maps, herbarium records) on Australian seagrasses. Existing initiatives such as Seagrass-Watch could cater for such an endeavor.

We have structured this chapter on a state-by-state basis. This might seem like an arbitrary decision given that seagrasses do not respond to state borders; however, management of seagrasses—including reporting of their change in cover and threats—generally occurs on a state-by-state basis. As pointed out by Larkum et al. (1989), seagrasses on the southeast coast of Australia do not conform to well-defined boundaries, especially where there are north and south flowing currents of warm and cold water, such as that which occurs in NSW and QLD due to the East Australian Current (EAC). For the purposes of this review, we classify the northern limit of the temperate zone in QLD by the Tropic of Capricorn, which intersects the continent at Rockhampton. Therefore, seagrasses occurring south of Rockhampton, QLD are considered temperate and included in this chapter.

## 2.2 Habitat Descriptions

Seagrasses of southeastern Australia occur within three main habitat types: estuaries, coasts (incl. gulfs and bays), and deep water (Fig. 2.2). Embedded within these main habitat types there are many sub-habitat types in which seagrasses occur, including: coastal lakes, dammed lagoons and rivers, open lagoons, estuaries, tidal rivers, arms, creeks, tributaries, sheltered beaches, bays, semi-exposed beaches and bays, exposed beaches and bays, and straits and channels. For simplicity, and because detailed information does not exist for all states, we have grouped seagrasses into the three major habitat types. The unique environmental conditions within each of these three main habitats affect the kinds of species that the different habitat types support.

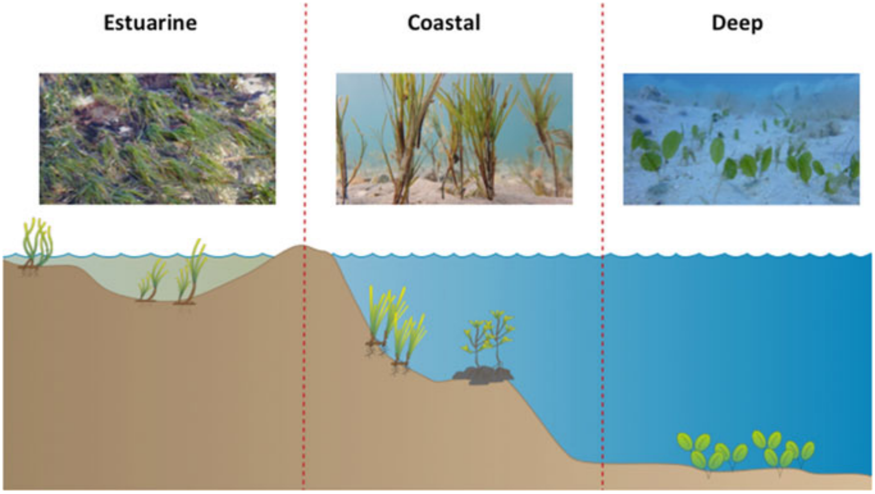

**Fig. 2.2** Conceptual diagram showing the main habitat types (estuarine, coastal and deep) for seagrasses in temperate QLD, NSW, VIC, and TAS. Note that estuarine and coastal seagrasses can occur in the intertidal or subtidal zone

An estuary has been defined as '*a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible*' (Potter et al. 2010). Seagrasses in southeastern Australia grow in a variety of estuary types (e.g. downed river valleys, intermittently closed or open lakes and lagoons—ICOLLs, strandplains, embayments, tidal creeks), although most occur in wave-dominated estuaries (Turner et al. 2004). The interaction of wave, tide, and rivers determine the formation of estuaries. For example, coastal lagoons (e.g. Tuggerah Lake, NSW) form in wave-dominated areas of the coast, where there is minimal river and tidal influence (Macreadie et al. 2015b), whereas drowned river valleys (e.g. Derwent River, TAS) are sculpted by freshwater flows (usually from receding glaciers) during times when sea levels were lower than present (Pritchard 1967). Because estuaries are dynamic by nature, their seagrass inhabitants are subjected to changing environmental conditions over short (e.g. seasonal) and long (e.g. El Nino Southern Oscillation or ENSO cycles) time scales (Macreadie et al. 2015a).

Coastal seagrasses in southeastern Australia mostly grow on soft, sandy sediments, although some species (e.g. *Amphibolis antarctica*) occur on reefs. In contrast to estuaries, coastal seagrasses are less often subjected to variable conditions, with perhaps the main exception being for those growing within intertidal rockpools (Fig. 2.3), which very much like estuaries are subjected to dramatic fluctuations in environmental conditions, including salinity, temperature, wind,

**Fig. 2.3** **a** A coastal embayment (Kitty Miller, VIC) with **b** intertidal *Zostera nigricaulis*

tides and waves. Coastal seagrasses in southeastern Australia are also subjected to nutrient and sediment runoff from the land, although this varies widely from location to location. Factors generally affecting the composition and distribution of seagrass species growing along the southeastern coast of Australia include: tidal range, proximity to land-based disturbances (e.g. runoff), and sediment movement.

Deep-water seagrasses are often defined as those occurring in depths greater than 15 m (Coles et al. 2009). The dominant genera that occur in deep-waters are the small-growth form species that can cope with low light levels and low wave energy, namely species of the *Halophila* genus. Deep-water seagrass species have received little attention relative to their shallow-water counterparts, probably because they are logistically more difficult to study, they occur in areas where there is less human activity, and because they are not considered to be as important (in terms of provision of ecosystem services) as shallow-water seagrasses. In fact, the very existence and spatial extent of deep-water seagrasses around Australia has only recently been acknowledged. Coles et al. (2009) estimated that Queensland's tropical deep-water seagrasses are among the most extensive on earth, occupying some 40,000 km$^2$ around the Great Barrier Reef. As for the existence and spatial extent of deep-water seagrasses within south eastern Australia, relatively little is known. The only studies, to our knowledge, that have reported deep-water seagrass in the region are by Ierodiaconou et al. (2007) in depths ranging from 15 to 35 m on a fine sand plateau in coastal waters of south-west Victoria. This species is widely distributed in deep-water across much of the Victorian coast (Ierodiaconou et al. 2007). Blake et al. (2012) reported *Zostera* spp. in deep water (typically around the 13–22 m depth) within the Otway, Central and Flinders bioregions, mainly in lower energy regions.

## 2.3 Species Distributions

In preparing this chapter on the biogeography of seagrasses in temperate Queensland, New South Wales, Victoria and Tasmania, we have followed the nomenclature supported by the taxonomic authority for Australia, the Australian Plant Census (APC) and the International Plant Names Index (IPNI), which maintain accurate records of vascular plants in Australia. Based on the APC/IPNI, we recognize the following species in temperate Australia, and in this chapter (Table 2.1).

Due to contention over the status of *Lepilaena* spp. and *Ruppia* spp. as a seagrass, as well as lack of information over the biogeography of *Lepilaena* spp., we have omitted *Lepilaena* spp. and *Ruppia* spp. from this chapter (as have many other seagrass books). There is very little information on *Lepilaena* spp. for southeastern Australia, or for the rest of Australia for that matter, and we would like to flag this as an important gap in knowledge that should be filled.

**Table 2.1** List of seagrass species occurring in temperature Australia and the geomorphic environment in which they occur

| Family | Species | QLD | NSW | Vic | Tas | Bays | Estuaries | Coasts |
|---|---|---|---|---|---|---|---|---|
| **Zosteraceae** | | | | | | | | |
| | *Zostera muelleri* Irmisch ex Asch. | x | x | x | x | x | x | |
| | *Heterozostera nigricaulis* J. Kuo | | x | x | x | x | | x |
| | *Heterozostera tasmanica* (G. Martens ex Asch.) Hartog | | | x | x | ? | | x |
| **Hydrocharitaceae** | | | | | | | | |
| | *Halophila australis* Doty & B.C. Stone | | x | x | x | x | | x |
| | *Halophila decipiens* Ostenf. | x | x | | | x | | x |
| | *Halophila minor* (Zoll.) Hartog | | ^ | | | | | |
| | *Halophila ovalis* (R.Br.) Hook.f. | x | ^ | | | x | x | x |
| | *Halophila spinulosa* (R.Br.) Asch. | x | | | | x | | x |
| **Cymodoceae** | | | | | | | | |
| | *Amphibolis antarctica* (Labill.) Sond. & Asch. ex Asch. | | | x | x | x | | x |
| **Posidoniaceae** | | | | | | | | |
| | *Posidonia australis* Hook. f. | | x | x | | x | x | |
| **Cymodoceaceae** | | | | | | | | |
| | *Halodule uninervis* (Forssk.) Boiss | x | x | | | x | x | x |
| | *Syringodium isoetifolium* (Asch.) Dandy | x | | | | x | | |
| | *Cymodocea serrulata* (R. Br.) Asch. & Magnus | x | | | | x | x | |
| | *Cymodocea rotundata* Asch. & Schweinf | x | | | | x | | x |

*x = present, ? = unknown, ^ = present but taxonomic uncertainty relating to species present*. For the current status of the genus *Heterozostera* see the Appendix to this volume

### *2.3.1 Temperate Queensland (QLD)*

The biogeographical climate of Southeast Queensland is defined as a transition zone from ‘subtropical’ to temperate. However, there is some debate about the use of the term ‘subtropical’ which can be interchanged with ‘warm temperate’. For the purposes of this chapter, we define the northern limit of the temperate zone on the east coast of Australia by the Tropic of Capricorn, which intersects at Rockhampton. Therefore, seagrasses found south of Rockhampton are considered temperate and thus considered here.

The seagrasses of temperate Queensland include approximately eight species from five genera (*Zostera*, *Halophila*, *Halodule*, *Syringodium* and *Cymodocea*) extending over the coastal area from the Capricorn coast near Rockhampton south to Moreton Bay near the border of New South Wales. The diversity of species in this region reflects the variety of habitats available, including coasts, bays, estuaries, lagoons, reefs and island systems (Carruthers et al. 2002). The majority of these habitats are also subjected to high volume summer rainfall, cyclones, severe storms, episodic pulses of nutrient-rich sediment, and macrograzers such as fish, dugongs and turtles that result in spatially and temporally variable seagrass meadows (Coles et al. 2009). Diversity is highest in northern Queensland, with a gradual decline in diversity moving south into the temperate zone (Coles et al. 2009).

There are large seagrass meadows surrounding the Capricorn region, including Port Curtis near Rockhampton and the Capricorn-Bunker Island group east of Gladstone. Gladstone Harbour (Port Curtis) contains areas of high seagrass value, with extensive meadows that were estimated at 120 km$^2$ in 2010 (Thomas et al. 2010). Further south in Hervey Bay, some of the largest seagrass meadows on the eastern Australian seaboard can be found, covering an area of over 2,300 km$^2$ (McKenzie et al. 2000). Closer to the New South Wales border, seven species of seagrass cover approximately 190 km$^2$ area within Moreton Bay and the surrounding waterways, including Pumicestone Passage to the north and the Gold Coast Broadwater to the south (Roelfsema et al. 2009, 2013).

#### 2.3.1.1 Zostera muelleri

*Zostera muelleri* is one of the most dominant meadow-forming seagrass species along the southeast Queensland coastline. These meadows are often recorded as *Zostera capricorni*, which is now recognised as a subspecies of *Z. muelleri* (Jacobs et al. 2006). This species is often found much further upstream than other species that are restricted to estuary entrances, and is assumed to be able to tolerate a wide variation in salinity, temperature and light regime (Williams et al. 2013). *Zostera muelleri* is recorded as the dominant intertidal and shallow-subtidal species on the Southern Queensland coast including Rockhampton, Gladstone, Hervey Bay and Moreton Bay where it is present in 70–80% of seagrass meadows (Thomas et al. 2010; Roelfsema et al. 2009, 2013). While significant declines of *Z. muelleri* subsp. *capricorni* have been recorded in southeast Queensland (Campbell and McKenzie 2004; Abal and Dennison 1996; Hyland et al. 1989), the meadows usually recovered within 3 years (Campbell and McKenzie 2004).

#### 2.3.1.2 *Halophila* spp.

*Halophila* species are frequently recorded in southeast Queensland as dominating the deeper subtidal waters (>5 m depth). Three species exist in this region: *H. ovalis*, *H. decipiens* and *H. spinulosa*, of which *H. ovalis* is the most common. All three species commonly co-occur in low density meadows, often intermixed with other species such as *Z. muelleri*. *Halophila ovalis* has a very wide environmental range and is found along the entire Queensland coastline. It can tolerate a range of salinities, depths and conditions and is often the first species to re-establish following a disturbance (Waycott et al. 2014).

*Halophila decipiens* and *H. spinulosa* are primarily tropical species but can be found in the temperate waters of southeast Queensland where they are commonly observed within sheltered bays and the entrances of open estuaries where tidal exchange is high (Williams et al. 2013; Waycott et al. 2014).

### *2.3.2 Halodule uninervis*

*Halodule uninervis* is primarily a tropical seagrass species and is most frequently found on shallow intertidal sand or mud banks in southern temperate Queensland, where it can tolerate large fluctuations in salinity (Waycott et al. 2014). This species forms dominant meadows in the intertidal and shallow subtidal areas all along the coast from Rockhampton to Moreton Bay (Coles et al. 2003). It is known to rapidly colonise a range of habitats, playing an important role in the stabilisation of sediments following disturbance (Waycott et al. 2014).

#### 2.3.2.1 Syringodium isoetifolium

*Syringodium isoetifolium* is generally found in patchy, mixed meadows within clear waters and on sandy substrates from the shallow intertidal to 15 m depth (Short et al. 2010; Waycott et al. 2014). In southern temperate Queensland, *S. isoetifolium* is only known to occur in mixed beds within Moreton Bay, alongside *Z. muelleri* and *H. ovalis*, where it is restricted to subtidal areas that maintain oceanic salinity (Young and Kirkman 1975). Unfortunately, the distribution of *S. isoetifolium* in Moreton Bay was significantly reduced by almost 100% following a major flooding event in 2011, with little recovery recorded over a year later (Hanington et al. 2014).

#### 2.3.2.2 Cymodocea spp.

Two species of the *Cymodocea* genus are found in southern temperate Queensland, *C. serrulata* and *C. rotundata*, although both are less well documented than the more dominant *Zostera*, *Halodule* and *Halophila* species listed above. Both species have a primarily tropical distribution and occur in similar habitats, although *C. serrulata* is also relatively common in warm temperate waters (den Hartog and Kuo 2006; Waycott et al. 2014), while *C. rotundata* is considered restricted to waters warmer than 20 °C in winter (Mukai 1993). There are numerous recordings of *C. serrulata* within Moreton Bay (Kirkman et al. 1997; Roelfsema et al. 2009, 2015), as well as further north towards the Capricorn coast where it is commonly found on muddy reef tops (Lee Long et al. 1993; Waycott et al. 2014). This species typically grows at 3–4 m depth in meadows that can appear very similar to smaller plants of the temperate species *Posidonia australis*; however *C. serrulata* is more tolerant of turbid environments (Waycott et al. 2014) and on the east coast of Australia these species are not known to co-occur.

*Cymodocea rotundata* is considered native to tropical Queensland (Waycott et al. 2004), although there are isolated reports of this seagrass growing as far south as Gladstone Harbour (Thomas et al. 2010). This species commonly occurs in the clear, low-nutrient waters of reef-associated habitats (Carruthers et al. 2002). Isolated patches of *C. rotundata* were identified for the first time in the warm temperate waters of Gladstone Harbour in 2009 on the leeward side of Facing Island (Thomas et al. 2010).

### 2.3.3 New South Wales (NSW)

The temperate coastline of New South Wales is characterised by its high wave-energy sandy beaches and strong southward flowing East Australia Current. As such, the majority of marine vegetation is restricted to the calmer waters of estuaries and bays. There are 184 recognised estuaries across the state (Roper et al. 2011), of which seagrass has been recorded within 111, with an estimated total area of 160 km$^2$ (Creese et al. 2009). There are four dominant seagrass genera found across the state, including *Posidonia*, *Zostera*, *Halophila* and *Ruppia*. There have also been reports of the tropical seagrass species, *Halodule uninervis*, located within Wallis Lake in central NSW.

The exact number of seagrass species occurring within NSW waters is often unclear. Historical reports have recorded species counts of between six and ten species (Kirkman 1997; Creese et al. 2009). This is due largely to taxonomical discrepancies and continually updated genetic technologies (Waycott et al. 2014). Despite fluctuations in the number of reported species, it is generally accepted that NSW is probably one of the least represented Australian states in regards to seagrass diversity and abundance (Kirkman 1997).

#### 2.3.3.1 Posidonia australis

*Posidonia australis* is the only member of the *Posidonia* genus found along the New South Wales coastline. Contrary to the more continuous *P. australis* meadows located on the west coast of Australia, those within NSW are primarily confined to the sheltered waters of geographically separated estuaries and bays (Waycott et al. 2014).

Only 11% of NSW estuaries are inhabited by *P. australis* (Creese et al. 2009). This is in part due to the high number of hyposaline coastal lagoons along the NSW coastline, which are considered unsuitable habitat for the species (Kirkman 1997). As such, *P. australis* meadows are more readily located within large, open estuaries and bays (often close to the mouths) where there is a regular tidal exchange (West et al. 1985; Creese et al. 2009).

Wallis Lake in central NSW is considered the northernmost range edge of the species on the east coast of Australia (Creese et al. 2009). It has been hypothesised that *P. australis* populations originally colonised the coastline of NSW from the south, which is supported by genetic diversity data suggesting that the low genetic diversity of *P. australis* found in Wallis Lake results from a potential founder effect associated with colonisation patterns and range edge effects (Evans et al. 2014).

The low genetic diversity and infrequent sexual reproduction of NSW *P. australis* meadows, combined with their geographic isolation potentially preventing contemporary gene flow has created some concern regarding the longevity of the species in this region (Evans et al. 2014). In addition, many of these meadows grow in highly urbanised estuaries and have thus undergone significant declines related to human impact (particularly from boat moorings; West 2012). As such, all *P. australis* meadows from Port Hacking to Wallis Lake were recently listed as endangered by the Australian Federal Government under the Environment Protection and Biodiversity Conservation Act.

#### 2.3.3.2 Zostera muelleri

*Zostera muelleri* is one of the most dominant seagrass species along the New South Wales coastline, occurring in 93% of estuaries (West 1983). Currently, *Z. muelleri* is the only recorded Zosteraceae species in this region, however, multiple species have previously been recorded including *Z. capricorni* and *Heterozostera tasmanica* (Kirkman 1997), although it is now recognised that *Z. capricorni* is synonymous with *Z. muelleri* (Waycott et al. 2014). Small meadows of *H. tasmanica* have been recorded growing as far north as Port Stephens in NSW (Kirkman 1997), however these reports suggest that this species was gradually being replaced by the more exposure tolerant *Z. muelleri* and was more likely to be found in oceanic waters rather than within estuaries (Kirkman 1997).

*Z. muelleri* occurs predominantly on marine sand, with higher coverage generally around 3 km back from the estuary entrance (Kirkman 1997). However, with a relatively high tolerance to exposure and variable salinity, *Z. muelleri* may also be found within feeder creeks and coastal lagoons. This species will readily recolonise following disturbance by storms or human activity, and is often found in areas where *Posidonia australis* once dominated.

#### 2.3.3.3 Halophila spp.

Three species of *Halophila* are found across the coastline of New South Wales; *H. australis*, *H. decipiens* and the *H. ovalis* 'complex'. *Halophila australis* has been recorded primarily within estuaries in southern New South Wales, with the northernmost population reported in Sydney Harbour (Port Jackson). The species was formerly treated as a subspecies of *H. ovalis* (den Hartog and Kuo 2006), but can be distinguished by the number of styles found on female flowers (six in *H. australis* and three in *H. ovalis*; Waycott et al. 2014).

*Halophila decipiens* occurs in both shallow and deep waters (>50 m depth; Waycott et al. 2014) across the length of the NSW coastline. In shallow waters it occurs primarily in estuaries of the Sydney region (for example, Botany Bay and Narrabeen Lagoon; West 1983). There is a lack of information regarding the deepwater distribution of this species in NSW waters.

In the temperate southern hemisphere, four species of *Halophila* are included within the *H. ovalis* 'complex'; *H. ovalis*, *H. euphlebia*, *H. ovata* and *H. minor* (Waycott et al. 2014). Of these, *H. ovalis* and *H. minor* have been recorded within NSW waters (Kuo 2005), and are thus grouped here as the *H. ovalis* 'complex' until further research can resolve the genetic, phenotypic and ecological variation among samples.

### *2.3.4 Victoria (VIC)*

The Victorian coast supports a range of habitats and features conspicuous large bays and inlets, including Port Phillip Bay, Western Port and Corner Inlet. These large bays are often protected from wind and wave energy and support the majority of Victoria's seagrass populations. In Port Phillip Bay, Western Port and Corner Inlet seagrass is the dominant structured habitat where *Zostera/Heterozostera*, *Halophila* and *Posidonia* make use of the stable conditions and sandy/muddy substrate to form extensive meadows that extend from the intertidal to deeper subtidal habitats. Seagrasses are also found along Victoria's open coast where dense patches of *Amphibolis antarctica* can be found in high energy reef habitats and *Zostera/Heterozostera* and *Halophila* in deeper offshore habitats to 35 m. The estuaries in Victoria's west and east support populations of *Zostera* and *Ruppia*. Overall 7 species of seagrass are found in Victoria (Blake et al. 2012; Waycott et al. 2014).

#### 2.3.4.1 Zostera spp.

*Zostera* and *Heterozostera* are the dominant genera of seagrass in Victoria forming large monospecific beds in bays, estuaries and the open coast. There are three species found in Victoria, *Z. muelleri*, *H. nigricaulis* and *H. tasmanica* (Waycott et al. 2014). The Zostera/Heterozostera species complex has undergone regular changes in taxonomic classification where *Heterozostera tasmanica* has been split into *H. tasmanica* and *H. nigricaulis* (Les et al. 2002; Kuo 2005). Taxonomic confusion combined with similarities in morphological structure and ecosystem function has led most habitat mapping studies to describe beds simply as *Zostera* spp. Each species however tends to be found in different environmental conditions; *Zostera muelleri* is found in intertidal and estuarine environment, *H. nigricaulis* is found in subtidal habitats in bays and inlets and *H. tasmanica* in deeper coastal locations up to 25 m deep. Therefore we have described *Zostera* species distributions in line with environmental conditions.

#### 2.3.4.2 Zostera muelleri

*Zostera muelleri* is common in Victoria, dominating intertidal and estuarine habitats. In Western Port and Corner Inlet *Z. muelleri* forms extensive meadows on the intertidal banks that are exposed at low tide. In the high intertidal these populations tend to be sparse with poor coverage but become denser as they enter the lower intertidal and subtidal (Monk et al. 2011; French et al. 2014). In contrast, estuarine population of *Z. muelleri* are found in intertidal and subtidal habitats to depths of 2.3 m at lengths of over 0.5 m (Ball and Blake 2009). *Zostera muelleri* is generally restricted to the lower reaches of the estuaries where salinities are greater, however, many of the estuaries in Victoria's west are intermittently closed to the ocean and *Z. muelleri* populations persist even when salinities are lower than 10 PSS (Ball and Blake 2009). It is found in all the major estuaries in both the east and west of Victoria including extensive meadows throughout the Gippsland Lakes (Roob and Ball 1997).

#### 2.3.4.3 Heterozostera nigricaulis

*Heterozostera nigricaulis* (for current status see the Appendix) is found from the shallow subtidal to depths of 10 m in Port Phillip Bay, Western Port and Corner Inlet where it forms large dense monospecific meadows (Roob et al. 1998; Blake and Ball 2001b; Blake et al. 2012). It is also found in protected coastal regions such as Kitty Miller Bay on Phillip Island and the Crags at Port Fairy where it grows in the lee of shallow reefs that provide protection from waves, and seaside harbors at Apollo Bay and Portland. In estuarine habitats *H. nigricaulis* is mostly absent but has been recorded at the entrance of some estuaries (Ierodiaconou and Laurenson 2002). There is also evidence of *H. nigricaulis* in deeper (5–15 m) coastal habitats

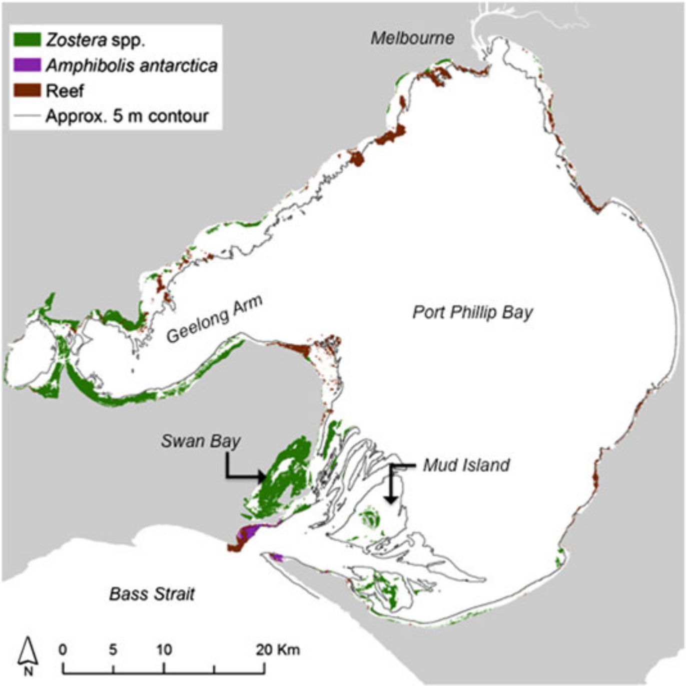

**Fig. 2.4** Seagrass distribution in Port Phillip Bay in 2000. The majority of seagrass occurs within Corio Bay and Swan Bay, two protected bays within the larger Port Phillip Bay (Blake and Ball 2001a)

but further sampling required to distinguish between it and *H. tasmanica* (D. Ierodiaconou, pers comms).

In Port Phillip Bay wave action and light/depth are the most important predictors of *H. nigricaulis* distribution where increasing depth and wave height limit seagrass colonization (Hirst et al. 2017; Hirst et al., in press). Within these limits *H. nigricaulis* distribution can be divided into two distinct habitats; protected bays such as Corio Bay and Swan Bay (Fig. 2.4) where wave action is limited and the sediment consists of fine grain sand with high organic matter content. In these habitats *H. nigricaulis* forms large, consistent meadows with long canopies. The second habitat includes areas exposed to greater wave action and consists of coarse sediment. At these sites *H. nigricaulis* is present in patchy mosaics that fluctuate over time, often moving in the swales of sand banks (Jenkins et al. 2015b).

#### 2.3.4.4 Heterozostera tasmanica

Found in deeper coastal habitats to 35 m, little is known about the distribution of *H. tasmanica* (Ierodiaconou et al. 2007) (for current status see the Appendix).

Coastal seagrass deeper than 15 m is common along the Victorian coast from Nelson in the west to Wilsons Promontory (Blake et al. 2012) and is assumed to be *H. tasmanica*. These populations tend to be found in fine sediment and there is speculation that they rely on input from river systems to provide nutrients (Ierodiaconou et al. 2007). Further research is needed to investigate the distribution, function and taxonomy of *H. tasmanica* in deep Victorian waters.

#### 2.3.4.5 Amphibolis antarctica

*Amphibolis antarctica* differs from other seagrasses as it is found growing on reefs, often in areas with high currents and wave activity. In Victoria, *Amphibolis antarctica* forms major beds found at entrance to Port Phillip Bay and Western Port where it forms dense monospecific or mixed algal beds (Blake et al. 2012). These habitats are typified by sandstone reef and high sediment movement. *A. antarctica* is found from the low intertidal to depths of 13 m depth. Small patches of *A. antarctica* are also found at Portland and Waratah Bay.

#### 2.3.4.6 Halophila australis

*Halophila australis* is primarily found on muddy sediment in the deeper margins of Victoria's major bays but has also been recorded at depths >8 m on the coast in sand patches amongst reef (Blake et al. 2012). The ephemeral nature of *H. australis* provides difficulties estimating its distribution and abundance. However, it has been estimated to cover over 2.5 km$^2$ in Western Port where it is prevalent in the east of the bay (Blake and Ball 2001b) and 158 km$^2$ in Corner Inlet (Roob et al. 1998).

#### 2.3.4.7 Posidonia australis

*Posidonia australis* is rare in Victoria being found exclusively in Corner Inlet and small patches at nearby Glennie Island and Little Waterloo Bay (Roob et al. 1998; Blake et al. 2012). It is the predominant seagrass and structured species in Corner Inlet where it forms dense beds on subtidal banks covering an estimated 30.7 km$^2$ (Ball et al. 2006). These beds are usually monospecific but can be found mixed with *Zostera* spp. *Posidonia australis* in Corner Inlet is disjunct from other *P. australis* populations and represents a refugia population from the last glacial maximum when it was isolated from western populations as Bass Strait became a land bridge to Tasmania (L. Sinclair, pers comm.).

### 2.3.5 Tasmania (TAS)

Tasmania is a unique state in Australia, being the only state independent of the island continent, and consisting of various islands of its own. Detailed analysis of Tasmanian seagrass distributions were observed and mapped in the 1980s by Hughes and Davis (1989b) and in the 1990s by Rees (1993). More recently, SEAMAP Tasmania at the Institute for Marine and Antarctic Studies at the University of Tasmania has been investigating and mapping seagrass habitats in Tasmania. SEAMAP is mapping the distribution of seabed habitat types in estuarine, coastal and marine waters of Tasmania through photographic, acoustic, biological and sediment sampling and consolidating all existing Tasmanian seabed habitat mapping data into a single Geographic Information System and relational database widely accessible for use by scientists, policy makers and other interested stakeholders (IMAS 2000–2016).

After an extensive review of habitat classifications for coastal Tasmania in his comprehensive work on Tasmanian seagrass biogeography, Rees (1993) characterized the coastal marine environment into 11 major habitat types based on geographic features (Rees 1993); however, as mentioned at the beginning of this chapter, the use of these categories have not been adopted by the other states, and to be consistent with the QLD, NSW, and VIC states, we have structured the biogeography of Tasmanian seagrasses by species. Besides geographic features, the biogeography of seagrass in Tasmania is also affected by climatic factors (including water and air temperatures, winds, and tides) and light availability and water quality (driven by turbidity and pollution, and salinity). Seagrass inhibit intertidal areas in some estuaries, but are predominantly subtidal throughout the state, occurring in all described habitat types.

In all, a total of five species of temperate seagrass were observed by Hughes and Davis (1989a) and the distributions of these were generally confirmed by Rees (1993) as occurring in Tasmania, including: *Amphibolis antarctica*, *Halophila australis*, *Heterozostera tasmanica*, *Posidonia australis* and *Zostera muelleri*. Since Rees (1993), *H. nigricaulis* was recognized as a separate species from *H. tasmanica* (Kuo 2005) and *H. nigricaulis* was subsequently observed as the dominant intertidal seagrass in Tasmania (T. Smith, pers. obs.). Additionally, *Ruppia maritima, Ruppia polycarpa* and *Ruppia megacarpa* are known to inhabitat inland lagoons, though specific mapping of these occurrences is lacking (Rees 1993) and therefore the biogeography of these species will not be discussed. Thus, there are a total of nine recognized seagrass species found in Tasmania at the present time. The most abundant seagrass species in Tasmania are *H. tasmanica* (which, following the acceptance of the new species and personal observations by experts is likely to be *H. nigricaulis*), and *Z. muelleri.* Due to Tasmanian island geography and clear trends in biological distribution, Tasmania was split by the Tasmanian Planning Commission (2009) into 9 coastal bioregions (Fig. 2.5). The distribution of seagrass species in these regions is summarized in Table 2.1. The species specific descriptions of distributions are summarized from Rees (1993) unless otherwise noted.

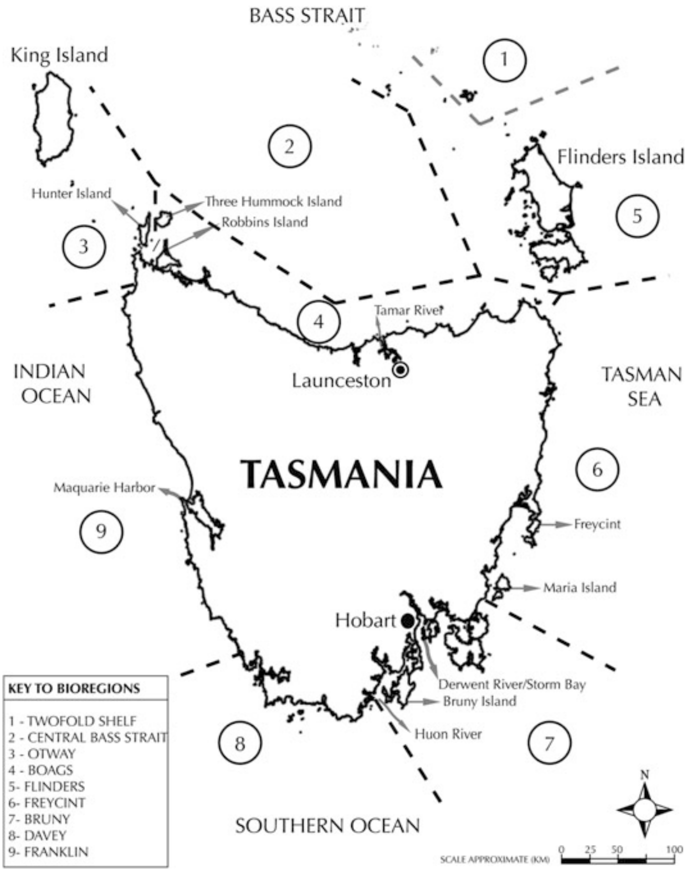

**Fig. 2.5** Map of Tasmanian bioregions adopted from State of the Environment Report: Tasmania (2009)

#### 2.3.5.1 Amphibolis antarctica

*Amphibolis antarctica* grows in fines sand areas of sheltered and semi-sheltered and exposed bays, straits and channels in coastal areas and in the Tamar River estuary of Tasmania. It has been sampled from depths of 2.5–5.5 m. It is not commonly found in association with any other seagrasses. Specific locations include several populations in the northern coast (Region 4), the southern end of Flinders Island (Region 5) and in two locations on the east coast (Region 6). The latter occurrences, confirmed on Maria's Island, appear to be the southern limit of the species range in Australia. The total mapped area of *Amphibolis antarctica* was 431 ha (Rees 1993).

#### 2.3.5.2 Halophila australis

*Halophila australis* can be found in monoculture or commonly in association with *Heterozostera tasmanica* in northern, eastern and predominately southern regions of Tasmania, specifically along the north coast (Region 4), east coast (Region 6 and 7) to a depth of 8 m, with some reports of plants as deep as 17 m. It usually grows in fine sand, but can tolerate some fine mud or mud sediments as well. It is primarily observed in sheltered bays, but is sometimes found in semi-exposed bays and deeper subtidal habitats of straits and channels. The total mapped area of *Halophila australis* was 1,212 ha (Rees 1993).

#### 2.3.5.3 Heterozostera tasmanica/Heterozostera nigricaulis

Due to the recent nomenclatural revisions described above and due to incongruences with these revisions and reported observations of the two species in Tasmania, published accounts of their separate geographic occurrences could not be verified for this chapter. As mentioned previously, some personal observations of species distribution have been made by the authors. In many cases it was confirmed that the species described in published reports was in fact *Heterozostera nigricaulis* rather than *Heterozostera tasmanica* (for current status of these species see the Appendix). Still, until a more detailed study can be completed on the distribution and overlap of these two species in Tasmania, the two species must be combined in reviewing biogeographical manuscripts for inclusion in this book. Therefore, in this section we will refer to these two species, by the single name referenced in published accounts to date as *Heterozostera tasmanica,* although the authors realize taxonomists now recognize two separate and identifiable species, each of which probably having disctinct biogeographies. Future studies should aim to separate and provide accounts of their variable biogeography.

*Heterozostera tasmanica* is the most widespread seagrass species in Tasmania, located in all the marine and estuarine bioregions (Regions 1–9) described above. It is most often found growing alone, but may also be found in association with other seagrasses. It has been observed in most coastal formation types with the exception of closed and semi-closed drainage basins, likely due to its intolerance of low salinity. This species favours sheltered bays with fine sands, but it is tolerant of fine mud and mud, and tidal currents in the channels of lagoons and estuaries. This species is noted to colonize areas of disturbance, including wave affected portions of *Posidonia* meadows. The most extensive populations are found in the south-eastern part of the state, where it is often found growing with *Halophila australis*. In the northeastern part of the state, including off Flinders Island, *Heterozostera tasmanica* can be found in association with *Posidonia australis* and in the south-west it can be found growing in association with *Zostera mulleri*. The species is not found above the low water mark and was found growing to the maximum depth of the survey, which was 10 m. The total mapped area of *Heterozostera tasmanica* was 8,182 ha (Rees 1993).

#### 2.3.5.4 Posidonia australis

*Posidonia australis* is the most abundant seagrass in Tasmania, covering 10,849 ha in limited parts of the state (Regions 3–5) in the Bass Strait (Rees 1993). These populations are likely to represent the southern distribution limit for this species in Australia. *Posidonia australis* favours sheltered to semi-sheltered bays, estuaries and channels with fine, sandy flat sediments. It can sometimes be found in sloping and higher energy beds where *Amphibolis antarctica* or more commonly *Heterozostera tasmanica* inhabit the tidal edge, thus protecting *Posidonia australis* on its wave affected borders. It was most often found in monospecific beds at depths between 2 and 5 m, and some at depths up to 9 m, though it was observed by Edgar (1984b) to be growing considerably deeper (20 m).

#### 2.3.5.5 Zostera muelleri

*Zostera muelleri* has been found in nearly all regions of Tasmania, with the exception of the west coast (Region 9). It tolerates a range of sediments, including fine sand, fine mud and mud in all coastal formation types except exposed coasts and channels and straits. It tolerates intertidal conditions, possibly up to 50% total exposure each day and was not observed at depths greater than 2.5 m in Tasmania. It is usually found in monospecific beds. The total mapped area of *Zostera muelleri* was 4,061 ha (Rees 1993).

## 2.4 Changes in Seagrass Distribution

Seagrass area and distribution varies in both space and time. Changes can reflect natural loss and recovery from extreme events where populations are unable to recover (see Chapter X 'Dynamics, thresholds, tipping points and loss of resilience in Australia seagrass ecosystems" for further information). Short-lived species such as *Halophila* grow opportunistically, often colonising an area quickly before dying off. Long-lived species such as *Posidonia* on the other hand tend to have more stable populations and are unlikely to vary in distribution over small time scales.

A global team of seagrass researchers collated data covering 125 years and 215 sites and estimated the total loss of areal seagrass coverage in the last century was approximately 29% (Waycott et al. 2009). They purport that the rate of loss has escalated 10-fold since the 1940s. It is currently estimated that net losses to seagrass cover are nearing 7% annually. A report completed for the IUCN Red List of Endangered Species by expert seagrass researchers found that 14% of seagrass species worldwide are at an elevated risk of extinction, primarily due to anthropogenic stressors.

In this section we provide case studies of losses and gains in seagrass cover for southeastern Australia.

### *2.4.1 Decadal Fluctuations in Port Phillip Bay seagrass linked to rainfall (VIC)*

Changing environmental conditions can have a major impact on seagrass distribution. In Port Phillip Bay *Zostera* coverage has fluctuated significantly over the previous 70 years (Fig. 2.6). Seagrass losses have coincided with drought conditions and reduced freshwater flows. *Zostera* in Port Phillip Bay is thought to be nutrient limited and decreased nutrient inputs as freshwater flows decrease have been found to cause large-scale seagrass die off (Hirst et al. 2017). Changing weather patterns also play a role in sediment suspension and redistributions particularly as predominant wind directions and storm frequency's change. Such changes can result in seagrass burial and is a major contributor to the distribution of seagrass in Port Phillip Bay (Jenkins et al. 2015a).

### *2.4.2 Warming-Induced Seagrass Loss from Western Port Bay (VIC)*

There have been substantial losses of seagrass habitats across southeastern Australia. These losses have occurred in a range of habitats and under various conditions, often reflecting natural fluctuations in seagrass cover as mentioned above. However, there have been instances of extreme and chronic seagrass loss that have shown little recovery. Many of these losses rely on anecdotal evidence from fishermen and other ocean users but there are several quantified instances of large seagrass loss (Parry 2010).

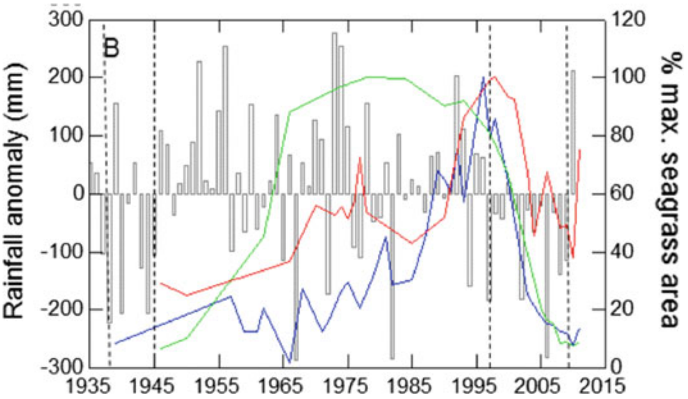

**Fig. 2.6** Changes in percent *Zostera* spp. seagrass cover at three sites in Port Phillip Bay from 1935 to 2012 (Roob and Ball 1997; Ball et al. 2014) overlaid on annual rainfall (Hirst et al., in press)

Western Port, Victoria has experienced gradual seagrass loss over the past 90 years (Parry 2010). Initial losses in the north were attributed deposition of sand and mud from drainage used for agriculture and land reclamation (Parry 2010). These losses started prior to 1939 and continued into the late 70s and early 80s Western Port experienced extreme seagrass losses (Parry 2010). It is estimated that 176 $km^2$ or between 49 and 92% of seagrass cover and over 85% of seagrass biomass was lost between 1973 and 1983 (Bulthuis et al. 1984; Parry 2010). The cause of these declines remains unclear but the most compelling argument is desiccation and heat stress (Bulthuis et al. 1984; Parry 2010). During the early 1980s the number of days experiencing extreme air temperatures (<30 °C) that coincided with low tides during the day was greater than any time over the previous 20 years (Parry 2010). On these days it is thought that intertidal seagrass was exposed to extreme conditions causing it to die off resulting in large seagrass losses.. These conditions were compounded by the increased height of seagrass meadows on the banks from years of sediment accumulation exposing the seagrass to even greater periods of stress (Bulthuis et al. 1984; Parry 2010). The total loss of seagrass in these areas of Western Port have released sediment into the water column and although there has been some recovery of seagrass in other areas (Blake and Ball 2001b) regions where there was extensive seagrass loss have remained turbid preventing recovery, equating to an alternative stable state of bare sand (Parry 2010).

### *2.4.3 Impacts of Floods and Dredging on Queensland Seagrasses (QLD)*

In northern temperate Queensland near to the Tropic of Capricorn and southern Great Barrier Reef, regional seagrass cover is considered stable or increasing since monitoring began in 2007 (GBRMPA 2011). There are recorded declines in seagrass cover at reef sites, although it should be noted that seagrass cover was less than 10% at these sites since monitoring began. Ongoing monitoring in Port Curtis and Rodds Bay has indicated that while there are large meadows of seagrass present, the total area significantly decreased following floods in 2011 (Sankey and Rasheed 2011). Additionally, estuarine meadows in the region are considered in poor condition, with seed banks and reproductive status also in a ‘poor’ state (GBRMPA 2011).

Gladstone is home to one of the largest export ports in Australia and is the focus of a rapid industrial expansion. As such, there is extensive industrial infrastructure close to the port, existing and proposed land reclamations, urban and industrial discharge and regular dredging within the harbour. While this poses a serious threat to the vulnerable extant seagrass meadows, most reports of significant seagrass decline have been attributed to major flood events (Thomas et al. 2010; McCormack et al. 2013).

Devastating seagrass losses have been recorded in Hervey Bay following flood and cyclone events in 1992 ($\sim$1000 km$^2$ lost; Preen et al. 1993) and 1999 (McKenzie et al. 2000). Seagrass completely disappeared from the shallow sub-tidal in late 1999 and took 30 months post-flood to fully recover (Campbell and McKenzie 2004).

Seagrasses within Moreton Bay have recorded steady declines since the 1940s (Kirkman 1978; Moss 1998; Dennison and Abal 1999). The Brisbane River flows directly into Moreton Bay and typically contains very high sediment and nutrient levels which can be elevated following floods (EHMP 2010), significantly impacting surrounding seagrass meadows (Fig. 2.7; Maxwell et al. 2015).

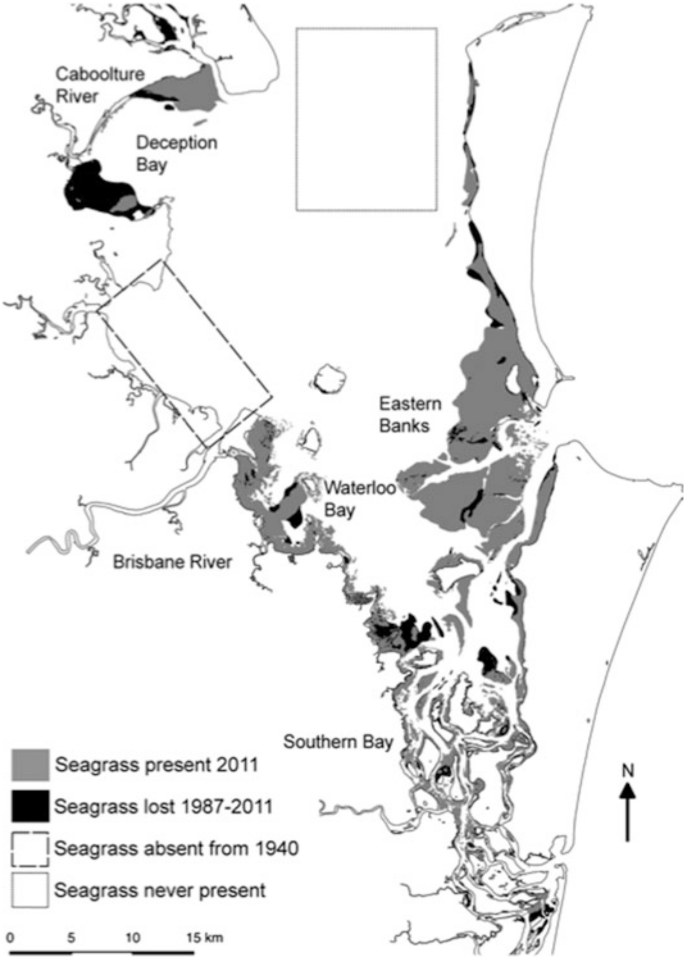

**Fig. 2.7** Changes in seagrass cover within Moreton Bay due to flooding and associated sediment and nutrient runoff (from Maxwell et al. 2015)

### 2.4.4 *Decline of Seagrasses in Urban Tasmania (TAS)*

Rees (1993) conducted extensive field mapping and areal photography analyses in all bioregions of Tasmania. He estimated overall loss of areal coverage of Tasmanian seagrass meadows to be approximately 25% over a 40-year period (1950–1990). Specific areas of recorded losses include: the Tamar Valley (−19%), Blackman Bay (−11%), Norfolk Bay (−58%), Duck Bay (−78%), Port Sorrell (−100%), Georges Bay (−48%), Spring Bay (−87%), Port Arthur (−37%), Wedge Bay and Parson's Bay (−61%), Pittwater (−94%), Ralph's Bay (100%), Northwest Bay (−38%), and finally, D'entrecasteaux Channel (−97%). Declines in cover continue, yet seagrasses remain unlisted under the Tasmanian Threatened Species Protection Act (Edgar et al. 2005).

The Derwent River and Hobart metropolitan areas have been the focus of more detailed ecological studies (Coughanowr et al. 2015). Losses to seagrass in the Bruny bioregion (Fig. 2.1, Region 7), which encompasses Hobart, include accounts of total losses of the meadows at Ralph's Bay, which were formerly mapped as a large area of dense seagrasses that has now experienced significant losses (Rees 1993). More recent mapping efforts reveal that seagrasses have still failed to recolonize this area (Lucieer et al. 2007).

### 2.4.5 *Decline of Seagrasses in Urban New South Wales (NSW)*

The coastline of New South Wales is one of the most densely populated regions of Australia, with many estuaries and bays located within metropolitan areas characterised by high levels of boating activity and associated infrastructure (e.g. boat moorings, marinas). The high wave-energy coastline of NSW unfortunately means that the majority of seagrass meadows are restricted to the same estuaries and bays, leaving them vulnerable to damage caused by ongoing anthropogenic disturbance (West 2012). Significant losses of seagrass area have been recorded in a number of estuaries surrounding the Sydney region since the 1940s (Larkum 1976; Larkum and West 1990; Walker and McComb 1992; Kirkman 1997; Meehan and West 2000; West 2012). These losses have been particularly alarming for the slow-growing species *Posidonia australis*, which can take decades to centuries to recolonise disturbed areas (Meehan and West 2000). As a result of ongoing declines, all *P. australis* meadows located between Wallis Lake and Port Hacking were recently listed as endangered by the Australian Federal Government under the Environment Protection and Biodiversity Conservation Act.

Some of the most well-documented seagrass declines on the NSW coast have been recorded since the 1930s in Botany Bay, an estuary that is characterised by decades of industrial development (Larkum 1976, 1983; Larkum and West 1990; Lord et al. 1999). Historical photography and field observations between 1930 and 1987 revealed total seagrass losses of 2500 ha (Larkum and West 1990; Kirkman 1997). These losses were attributed to a multitude of factors, including industrial and residential development in the catchment area, dredging at the bay's entrance and overgrazing by sea urchins (Larkum and West 1990). Some of the most serious losses appear to have been caused by light reduction in the water column, resulting from increased turbidity associated with eutrophication, dredging and development (Larkum 1983; Larkum and West 1990). Extensive dredging of the entrance to Botany Bay also resulted in an increase in wave height, which lead to the increased erosion of seagrass meadows (particularly during storms) and reduced leaf biomass of *P. australis* by up to 70% (Larkum and West 1990). Compounding these events, prawn trawling, industrial dispersants and hot water effluent from Bunnerong Power Station provided additional stressors within Botany Bay during this time (Larkum and West 1983; Kirkman 1997).

Further losses of *P. australis* and *Zostera muelleri* subsp. *capricorni* have been documented in Botany Bay since 1987 (Lord et al. 1999; SMEC 2003; West 2012). The construction of a runway extension at Sydney airport in 1994 resulted in a loss of 18 ha of *Z. muelleri* and 5 ha of *P. australis* (Lord et al. 1999). In 2004, further seagrasses losses were documented following the construction of an additional runway at Sydney airport (3.85 ha lost; SMEC 2003) as well as extensive dredging and filling of sand for a local beach nourishment project (13.73 ha lost; SMEC 2003). More recently, damage caused by boat propellers within *P. australis* meadows has been observed at Bonna Point (West 2012), and damage caused by boat moorings and the laying of submarine electricity cables has been observed within *P. australis* meadows at the western end of Silver Beach (Fig. 2.8, Evans et al. in press). Within-meadow fragmentation can be easily overlooked by current mapping technologies (Creese et al. 2009), but it is recognised that 'holes' within meadows caused by boat moorings or propellers can cause substrate instability and erosion (Macreadie et al. 2014b; Macreadie et al. 2015c), ultimately leading to large-scale losses (Larkum 1976; West 2012).

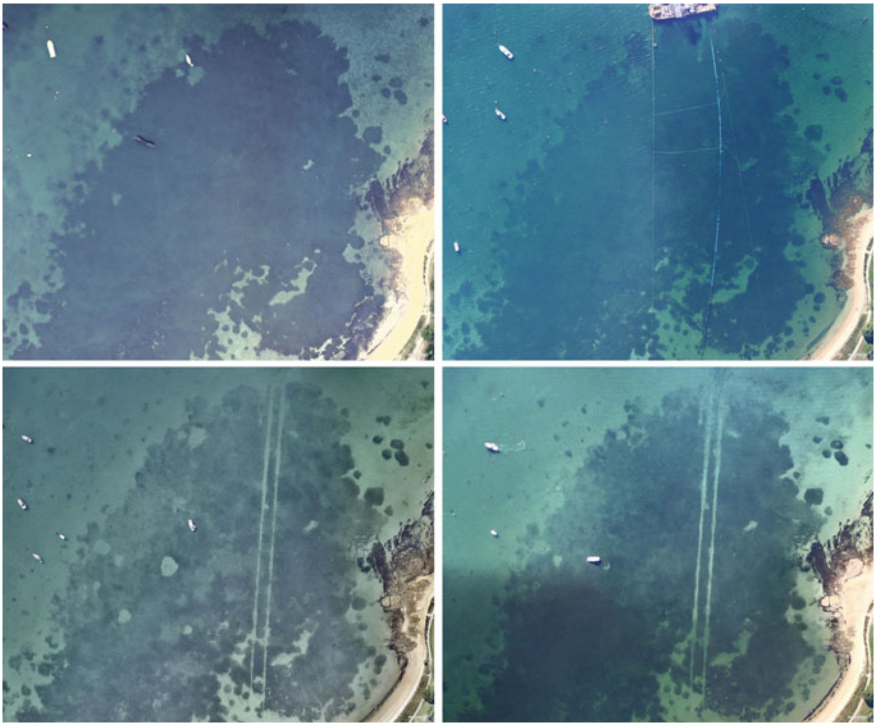

**Fig. 2.8** Aerial imagery taken from Nearmap Australia of a *Posidonia australis* meadow at Silver Beach, Botany Bay, showing the impact of boat moorings and power cable burial after four years (from left to right: original meadow in Apr 2010; initial construction first seen in Aug 2010; distinct damage left from cabling in Jul 2012; negligible recolonization in Sep 2014; Evans et al. in press)

## 2.5 Conclusions

The southeast coast of Australia is some to vast meadows of seagrass with high species diversity. In this chapter we have provided the most up-to-date information of the biogeography of seagrasses in temperate QLD, NSW, VIC, and TAS. At the present time, we are unable to provide high-resolution information for all locations due to limited information. We hope that more information will become available as the importance of seagrasses and their ecosystem services become more widely recognised (Lavery et al. 2013; Tuya et al. 2014; Campagne et al. 2015), and as remove sensing techniques become more affordable and more accurate for mapping submarine habitats (Macreadie et al. 2014a).

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# Chapter 3
# Seagrasses of Southern and South-Western Australia

**Kieryn Kilminster, Renae Hovey, Michelle Waycott and Gary A. Kendrick**

**Abstract** The coastal waters of southern and south-western Australia are home to almost 30,000 km$^2$ of seagrass, dominated by temperate endemic species of the genera *Posidonia* and *Amphibolis.* In this region, seagrasses are common in estuaries and sheltered coastal areas including bays, lees of islands, headlands, and fringing coastal reefs. Additionally, extensive meadows exist in the inverse estuaries of the Gulfs in South Australia, and in Shark Bay in Western Australia. This chapter explores (i) how geological time has shaped the coastline and influenced seagrasses, (ii) present day habitats and drivers, (iii) how biogeography patterns previously reported have been altered due to anthropogenic and climate impacts, and (iv) emerging threats and management issues for this region. Species diversity in this region rivals those of tropical environments, and many species have been found more than 30 km offshore and at depths greater than 40 m. Seagrasses in this region face a future of risk from multiple stressors at the ecosystem scale with

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coastal development, eutrophication, extreme climate events and global warming. However, our recent improved understanding of seagrass recruitment, restoration and resilience provides hope for the future management of these extraordinary underwater habitats.

## 3.1 Introduction

The diverse and expansive seagrass meadows of southern and south-western Australia create stunning underwater landscapes. Seagrasses in this region are recognised as a temperate biodiversity hotspot, with species diversity rivalling those of tropical environments (Carruthers et al. 2007). From Shark Bay to the western edge of the Great Australian Bight, seagrasses occupy an estimated 20,000 km$^2$ (Walker 1991). The coastal waters of South Australia are home to an additional 9,612 km$^2$ with more than 80% of this seagrass found within the Spencer Gulf (5,520 km$^2$) and the Gulf of St Vincent (2,440 km$^2$) (Edyvane 1999). These temperate meadows are often dominated by endemic *Posidonia* and *Amphibolis* species with high biomass (Fig. 3.1).

Species distributions are broadly known in South Australia (see Chap. 1 and the Appendix of this volume for genus distributions, plus Shepherd and Robertson 1989; Kirkman 1997). *Posidonia* is the dominant genus in terms of spatial coverage, with *P. angustifolia*, *P. australis*, and *P. sinuosa* being the most abundant species within the genus. The upper parts of both Spencer Gulf and Gulf St Vincent

**Fig. 3.1** Southern Fiddler ray within a *Posidonia sinuosa* meadow at Rottnest Island, Western Australia

have extensive tidal flats that are dominated by *P. australis* and *Zostera/Heterozostera* species (for current status of *Heterozostera* see the Appendix of this volume). Within the gulfs and bays around South Australia, seagrasses are generally restricted to depths of <20 m (Shepherd and Robertson 1989; Edyvane 1999). However, in the clearer waters of Investigator Strait, some offshore islands, and at the base of cliffs on the west coast of Eyre Peninsula, seagrasses grow to depths of 30 m or more (Shepherd and Robertson 1989).

In temperate Western Australia, seagrasses occupy shallow coastal habitat (Walker 1991), in water depths ranging from the intertidal to >50 m. Seagrasses occur in a range of habitats from wave-exposed sandbanks to sheltered bays, lagoons and estuaries (Carruthers et al. 2007). They grow predominantly on sand from 1 to 35 m depth (Cambridge and Kuo 1979), but also on deep rock to over 50 m deep (e.g. *Thalassodendron pachyrhizum*), and shallow estuarine mud and sand flats. Across southern temperate Australia, *Halophila australis* is endemic and is likely the only *Halophila* species occurring across the region immediately to the east of the Great Australian Bight, to Tasmania.

Along the southwest coast of Australia, seagrass habitats are heavily influenced by exposure to ocean swells and large-scale sand movement. *Amphibolis griffithii* has higher water baffling capacity than *Posidonia australis*, *P. sinuosa* or mixed *Posidonia* meadows (van Keulen and Borowitzka 2002). *Amphibolis antarctica* meadows have been shown to reduce water flows from 50 to 2–5 cm $s^{-1}$ (Verduin and Backhaus 2000). The *P. ostenfeldii* group of species typically form patchy meadows with mixed species in open-ocean or rough water sublittoral habitats (Campey et al. 2000). They are characterised by their long, thick, leathery leaves and long leaf sheaths that are deeply buried. Their ability to withstand ocean swell is because, unlike the *Posidonia australis* group, their rhizomes grow vertically instead of horizontally. These characters appear to be associated with strong wave movement and mobile sand substratum typical of the environments in which they are found (Kuo and Cambridge 1984).

The distribution of seagrasses around Australia was described in Larkum et al. (1989). Rather than revisit this earlier work on biogeography, which has remained relatively unchanged for this region, we explore aspects of new knowledge which now shape our understanding of seagrasses of southern and south-western Australia.

Specifically this chapter will describe:

(i) how geological time has shaped the coastline and influenced seagrasses,
(ii) present day seagrass habitats and drivers,
(iii) anthropogenic and climate change pressures which have altered biogeography patterns previously reported, and
(iv) emerging threats and management issues for this region.

Several case studies are discussed within this chapter, and Fig. 3.2 provides a map of seagrass in each of these locations.

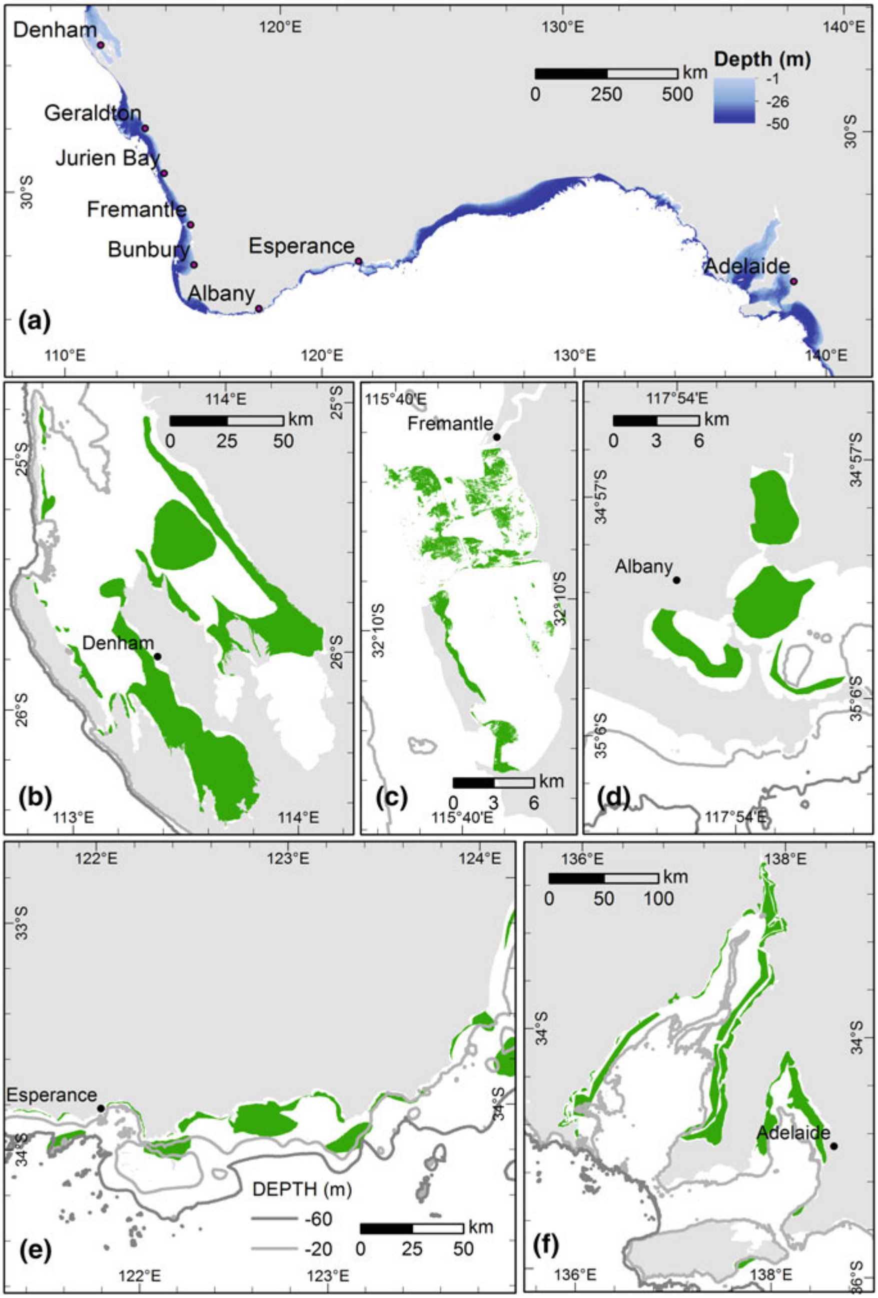


**Fig. 3.2** Map of region and case-study areas. **a** Potential areas in southern and south-western where water depth is likely to be suitable for seagrass habitat, and seagrass distribution in **b** Shark Bay, **c** Owen Anchorage and Cockburn Sound, **d** Albany harbours, **e** Recherche Archipelago and, **f** Gulf of St Vincent and Spencer Gulf

## 3.2 The Forces Shaping Seagrasses and the Coastline over Geological Time

Modern day lineages of seagrasses evolved some 60 + million years ago (Waycott et al. 2018, Chap. 5, this volume). Since this time, global sea level has fluctuated significantly, however seagrasses have been able to adapt to the rate of change in sea level (Orth et al. 2006). The modern day coastline of southern and south-western Australia became stable approximately 5,000 years ago (Fig. 3.3).

Rottnest Island, approximately 10 nautical miles offshore from Fremantle in Western Australia provides an excellent example of how the changing coastline has created habitats for seagrass. Rottnest Island is comprised of coastal Quaternary carbonate Aeolian dune complex and was joined to the mainland some 7,000 years ago. There are multiple drowned shorelines creating shoreline parallel ridges and reefs between Rottnest and the present-day Western Australian coast, and these sedimentary successions are very sensitive to erosion and sediment reworking (Richardson et al. 2005; Brooke et al. 2014). Sheltered waters provided by these reefal systems have favoured seagrasses with *Posidonia* and *Amphibolis* species forming patchy to continuous meadows, while seagrasses with reinforced fibres in their leaves (*P. ostenfeldii* complex) or wiry stems (*Amphibolis* species) dominate in more exposed waters (Carruthers et al. 2007). The high endemism of seagrasses in this region perhaps reflects the tectonic and geological stability of the region over the last 50 million years or so, allowing specialisation of seagrasses to occur.

The local Aboriginals, the Nyoongar people, have cultural narratives which describe the sea level rise which occurred separating Rottnest (or *Wadjemup*) from the mainland (Robertson et al. 2016). Similar stories exist in South Australia for the Jaralde people regarding Kangaroo Island and the Narrangga people regarding Spencer Gulf, likely to be associated with sea level rises between 10 and 12,000 years ago (Reid et al. 2014).

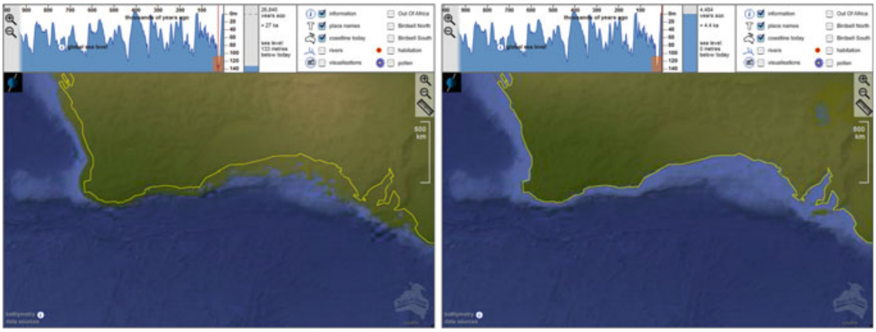


**Fig. 3.3** Coastline of south-west Australia approximately 27,000 years ago (left) and coastline stabilised approximately 5,000 years ago to current position (right) (Images from http://sahultime.monash.edu.au)

Seagrasses have themselves altered this coastline by the in situ generation and trapping of carbonate sediments, derived in part from the calcareous algal epiphytes living on seagrass blades. This is one aspect which have earned seagrasses the title of ‘ecosystem engineers’—sensu Jones et al. (1997). A study of the coast in Geraldton, Western Australia revealed fine modern skeletal sands within 2 km of shore were dominated by modern bioclasts (Fig. 3.4) living in association with seagrass meadows (Tecchiato et al. 2016). The Australian coast was divided into three major sediment provinces by Short (2010), with the south and west coast described as carbonated-dominated. Carbonate sediment makes up approximately 70% of the beach sand in this region, with the exception of the south-western tip from Augusta to Bremer Bay, where carbonate sediments were approximately 30% (Short 2010). Calcareous sediments, made up of skeletal remains of bivalves, benthic foraminifera, bryozoans, coralline algae and echinoids, also dominate within Spencer Gulf in South Australia (O’Connell et al. 2016).

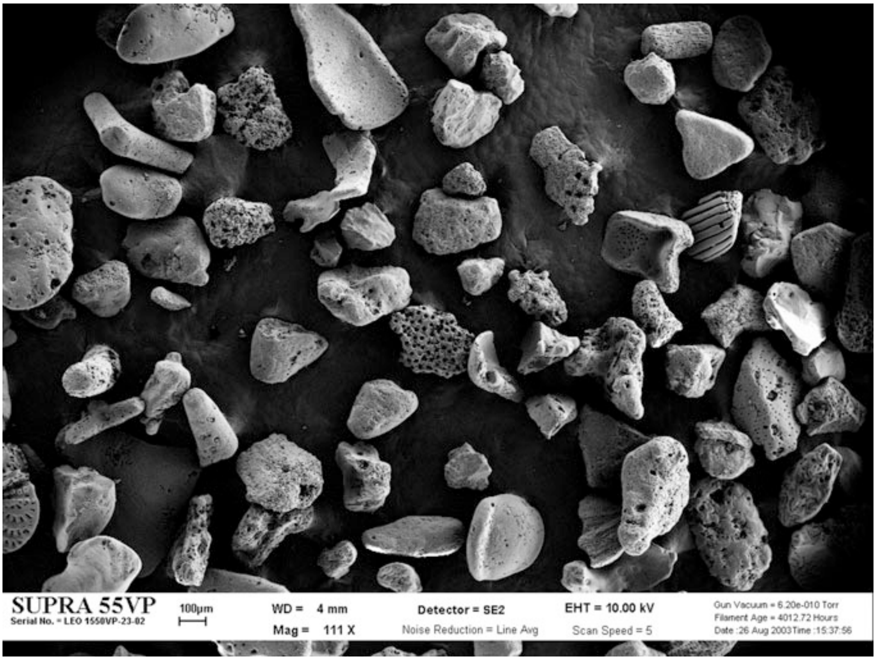


**Fig. 3.4** Sediment grains from Western Australia viewed by scanning electron microscopy at 111 × magnification clearly showing skeletal makeup of the coastal sands

## 3.3 Present Day Seagrass Habitats and Drivers

Seagrasses in southern and south-western Australian waters play important roles providing habitat for many fish and crustaceans, including commercially and recreationally important species such as King George whiting (Connolly 1994; Connolly and Jones 1996; Connolly et al. 1999; Hyndes et al. 1999; Bryars 2003; Bloomfield and Gillanders 2005). They support a large range of biodiversity, including molluscs, and epiphytic plants and algae (Keough and Jenkins 1995), and stabilize coastal sediments, trapping sediments, and preventing coastal erosion (Keough and Jenkins 1995; Westphalen et al. 2004). Carbon export from seagrass meadows to adjacent habitats may act as ecological subsidies (Connolly et al. 2005; Hyndes and Lavery 2005) and recently, attention has been given to their role in carbon burial and sequestration (Fourqurean et al. 2012; Lavery et al. 2013; Serrano et al. 2014; Marbà et al. 2015).

Seagrasses grow on sediments in intertidal and subtidal waters, wherever sufficient light and favourable hydrodynamic conditions exist. In this region, seagrasses are common in estuaries and sheltered coastal areas including bays, lees of islands, headlands, and fringing coastal reefs (Carruthers et al. 2007). The inverse estuaries of the Gulfs in South Australia, or in Shark Bay in Western Australia are also home to extensive seagrass meadows (Walker et al. 1988; Edyvane 1999).

Carruthers et al. (2007) described seagrass habitats for south-west and south-coast Western Australia as 'sheltered', 'exposed' and 'estuarine' habitats. This habitat classification is extended to South Australian waters with the inclusion of 'inverse estuary' to account for the habitats found within the gulfs. Table 3.1 provides a description of habitat type with seagrass assemblages commonly found in each region. Conceptual diagrams (Figs. 3.5, 3.6 and 3.7) present this information diagrammatically. Note, the natural break in the habitat types occurs at the Great Australian Bight, so is not explicitly described by State boundaries. The majority of seagrasses in the marine environments of south and south-western Australia are described as enduring, persistent seagrass meadows, while those in estuarine environments, particularly the bar-built estuaries, may have a mix of transitory, colonising seagrass meadows (sensu Kilminster et al. 2015). Dominant meadow types are also provided in Table 3.1 for each habitat found with these regions.

The sheltered waters of southern and south-western Australia are usually dominated by *Posidonia* and *Amphibolis* spp., both forming large, dense, enduring meadows. On the south-west coast, *Halophila ovalis*, *H. decipiens*, *Heterozostera nigricaulis*, *H. polychlamys*, and even sometimes *Syringodium isoetifolium* tend to occur as an understory to the larger-bodied seagrasses (Kendrick et al. 1999; Carruthers et al. 2007), and they may be first to recolonise sediments from blowouts following storms (Kirkman and Kuo 1990) or boat mooring damage (Walker et al. 1989). In southern Australia, sheltered waters are usually dominated by *P. australis*, while in deeper waters *P. sinuosa*, *P. angustifolia*, *A. antarctica* and *A. griffithii* are present (Edyvane 1999).

**Table 3.1** Description of habitat types and commonly found seagrass assemblages within each sub-region of southern and south-western Australia

| Region | Exposure and type | Sediment type | Seagrass assemblages (dominant meadow forming species in bold) | Dominant species type | Dominant meadow form | Example locations |
|---|---|---|---|---|---|---|
| South-west WA | Embayment | Carbonate | ***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>***Posidonia australis***<br>***Posidonia sinuosa***<br>*Syringodium isoetifolium*<br>*Halophila ovalis*<br>*Halophila australis*<br>*Halophila decipiens*<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring | Safety Bay, Geographe Bay, Cockburn Sound |
| South-west WA | Exposed coastline | Carbonate | ***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>***Posidonia australis***<br>***Posidonia coriacea***<br>***Posidonia sinuosa***<br>*Posidonia angustifolia*<br>*Thalassodendron pachyrhizum*<br>*Halophila ovalis*<br>*Halophila australis*<br>*Halophila decipiens*<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring, rarely transitory | Marmion Marine Park, Jurien Marine Park, Owen Anchorage |
| South-west WA | Sheltered estuary | Silicate | ***Halophila ovalis***<br>***Ruppia megacarpa***<br>*Zostera mulleri*<br>*Posidonia australis*<br>*Halophila decipiens* | Colonising | Enduring and transitory | Swan-Canning, Peel-Harvey Leschenault |

(continued)

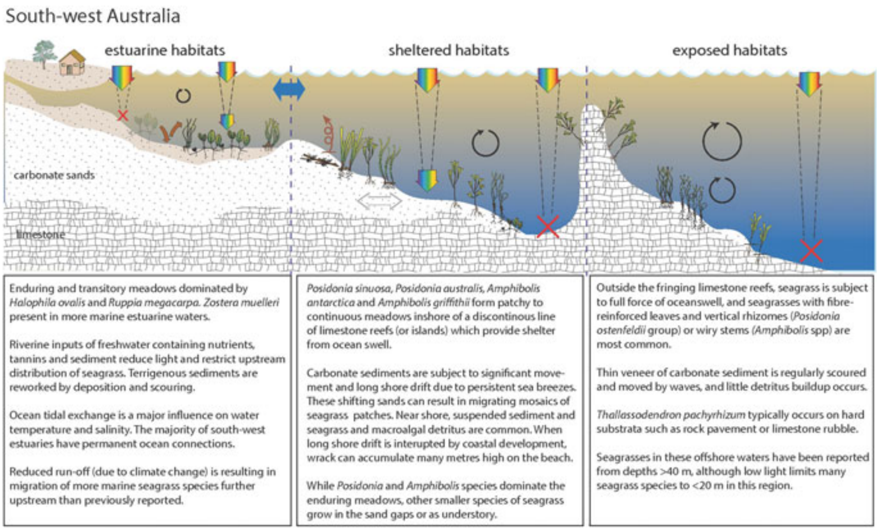
**Table 3.1** (continued)

| Region | Exposure and type | Sediment type | Seagrass assemblages (dominant meadow forming species in bold) | Dominant species type | Dominant meadow form | Example locations |
|---|---|---|---|---|---|---|
| South Coast WA | Embayment | Silicate | ***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>***Posidonia sinuosa***<br>***Posidonia ostenfeldii* complex**<br>*Posidonia australis*<br>*Posidonia angustifolia*<br>*Halophila ovalis*<br>*Halophila australis*<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring | King George Sound, Two Peoples Bay |
| South Coast WA | Exposed coastline | Carbonate | ***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>***Posidonia sinuosa***<br>***Posidonia australis***<br>***Posidonia angustifolia***<br>***Posidonia ostenfeldii* complex**<br>*Thalassodendron pachyrhizum*<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring | Esperance |
| South Coast WA | Sheltered estuary | Silicate | ***Ruppia megacarpa***<br>***Posidonia australis***<br>*Posidonia sinuosa*<br>*Amphibolis antarctica*<br>*Amphibolis griffithii*<br>*Halophila australis*<br>*Halophila ovalis*<br>*Halophila decipiens*<br>*Zostera mulleri* | Persistent, opportunistic and colonising | Enduring and transitory | Oyster Harbour, Walpole-Nornalup, Wilson Inlet, Oyster Harbour |

(continued)

**Table 3.1** (continued)

| Region | Exposure and type | Sediment type | Seagrass assemblages (dominant meadow forming species in bold) | Dominant species type | Dominant meadow form | Example locations |
|---|---|---|---|---|---|---|
| South Coast SA | Sheltered inverse estuary | Carbonate | ***Posidonia australis***<br>***Posidonia angustifolia***<br>*Amphibolis antarctica*<br>*Amphibolis griffithii*<br>*Heterozostera nigricaulis*<br>*Halophila australis* | Persistent | Enduring | Upper Gulf of St Vincent, Upper Spencer Gulf |
| South coast SA | Disconnected embayment/ estuary | Silicate | ***Ruppia megacarpa***<br>***Ruppia tuberosa***<br>*Zostera muelleri* | Colonising | Transitory and enduring | The Coorong |
| South coast SA | Embayment | Carbonate | ***Posidonia australis***<br>***Posidonia sinuosa***<br>***Posidonia angustifolia***<br>***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>*Halophila australis*<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring | Adelaide waters, Emu Bay, Fowlers Bay |
| South coast SA | Exposed coastline | Carbonate | ***Amphibolis antarctica***<br>***Amphibolis griffithii***<br>***Posidonia australis***<br>***Posidonia angustifolia***<br>***Posidonia ostenfeldii* complex**<br>*Heterozostera nigricaulis*<br>*Heterozostera polychlamys* | Persistent and opportunistic | Enduring | Offshore island—Pearson Island, Flinders Island |



Enduring and transitory meadows dominated by *Halophila ovalis* and *Ruppia megacarpa*. *Zostera muelleri* present in more marine estuarine waters.

Riverine inputs of freshwater containing nutrients, tannins and sediment reduce light and restrict upstream distribution of seagrass. Terrigenous sediments are reworked by deposition and scouring.

Ocean tidal exchange is a major influence on water temperature and salinity. The majority of south-west estuaries have permanent ocean connections.

Reduced run-off (due to climate change) is resulting in migration of more marine seagrass species further upstream than previously reported.

*Posidonia sinuosa*, *Posidonia australis*, *Amphibolis antarctica* and *Amphibolis griffithii* form patchy to continuous meadows inshore of a discontinous line of limestone reefs (or islands) which provide shelter from ocean swell.

Carbonate sediments are subject to significant movement and long shore drift due to persistent sea breezes. These shifting sands can result in migrating mosaics of seagrass patches. Near shore, suspended sediment and seagrass and macroalgal detritus are common. When long shore drift is interupted by coastal development, wrack can accumulate many metres high on the beach.

While *Posidonia* and *Amphibolis* species dominate the enduring meadows, other smaller species of seagrass grow in the sand gaps or as understory.

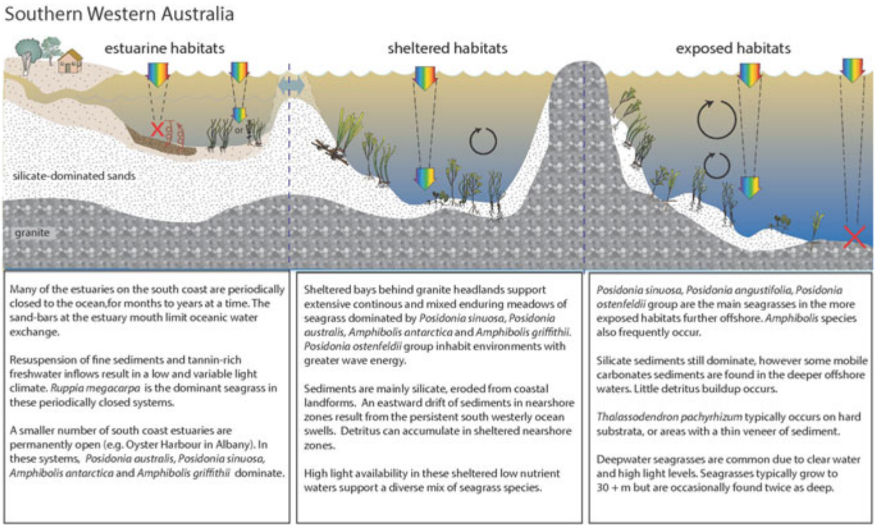
Outside the fringing limestone reefs, seagrass is subject to full force of oceanswell, and seagrasses with fibre-reinforced leaves and vertical rhizomes (*Posidonia ostenfeldii* group) or wiry stems (*Amphibolis* spp) are most common.

Thin veneer of carbonate sediment is regularly scoured and moved by waves, and little detritus buildup occurs.

*Thallassodendron pachyrhizum* typically occurs on hard substrata such as rock pavement or limestone rubble.

Seagrasses in these offshore waters have been reported from depths >40 m, although low light limits many seagrass species to <20 m in this region.

**Fig. 3.5** Seagrass habitats in south-west Australia



Many of the estuaries on the south coast are periodically closed to the ocean,for months to years at a time. The sand-bars at the estuary mouth limit oceanic water exchange.

Resuspension of fine sediments and tannin-rich freshwater inflows result in a low and variable light climate. *Ruppia megacarpa* is the dominant seagrass in these periodically closed systems.

A smaller number of south coast estuaries are permanently open (e.g. Oyster Harbour in Albany). In these systems, *Posidonia australis*, *Posidonia sinuosa*, *Amphibolis antarctica* and *Amphibolis griffithii* dominate.

Sheltered bays behind granite headlands support extensive continous and mixed enduring meadows of seagrass dominated by *Posidonia sinuosa*, *Posidonia australis*, *Amphibolis antarctica* and *Amphibolis griffithii*. *Posidonia ostenfeldii* group inhabit environments with greater wave energy.

Sediments are mainly silicate, eroded from coastal landforms. An eastward drift of sediments in nearshore zones result from the persistent south westerly ocean swells. Detritus can accumulate in sheltered nearshore zones.

High light availability in these sheltered low nutrient waters support a diverse mix of seagrass species.

*Posidonia sinuosa*, *Posidonia angustifolia*, *Posidonia ostenfeldii* group are the main seagrasses in the more exposed habitats further offshore. *Amphibolis* species also frequently occur.

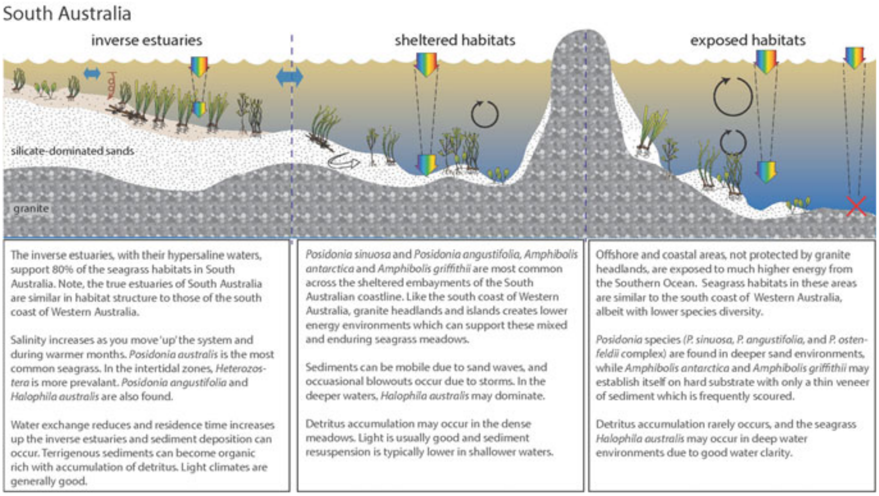
Silicate sediments still dominate, however some mobile carbonates sediments are found in the deeper offshore waters. Little detritus buildup occurs.

*Thalassodendron pachyrhizum* typically occurs on hard substrata, or areas with a thin veneer of sediment.

Deepwater seagrasses are common due to clear water and high light levels. Seagrasses typically grow to 30 + m but are occasionally found twice as deep.

**Fig. 3.6** Seagrass habitats in southern Australia, from Cape Leeuwin to Spencer Gulf

Enduring *Posidonia* and *Amphibolis* spp. still feature in the exposed waters of southern and south-western Australia, however those *Posidonia* species more tolerant of rough conditions, such as *P. coriacea* and the *P. ostenfeldii* complex, may form patchy meadows (Campey et al. 2000; Carruthers et al. 2007). Western



The inverse estuaries, with their hypersaline waters, support 80% of the seagrass habitats in South Australia. Note, the true estuaries of South Australia are similar in habitat structure to those of the south coast of Western Australia.

Salinity increases as you move 'up' the system and during warmer months. *Posidonia australis* is the most common seagrass. In the intertidal zones, *Heterozostera* is more prevalant. *Posidonia angustifolia* and *Halophila australis* are also found.

Water exchange reduces and residence time increases up the inverse estuaries and sediment deposition can occur. Terrigenous sediments can become organic rich with accumulation of detritus. Light climates are generally good.

*Posidonia sinuosa* and *Posidonia angustifolia, Amphibolis antarctica* and *Amphibolis griffithii* are most common across the sheltered embayments of the South Australian coastline. Like the south coast of Western Australia, granite headlands and islands creates lower energy environments which can support these mixed and enduring seagrass meadows.

Sediments can be mobile due to sand waves, and occuasional blowouts occur due to storms. In the deeper waters, *Halophila australis* may dominate.

Detritus accumulation may occur in the dense meadows. Light is usually good and sediment resuspension is typically lower in shallower waters.

Offshore and coastal areas, not protected by granite headlands, are exposed to much higher energy from the Southern Ocean. Seagrass habitats in these areas are similar to the south coast of Western Australia, albeit with lower species diversity.

*Posidonia* species (*P. sinuosa, P. angustifolia,* and *P. ostenfeldii* complex) are found in deeper sand environments, while *Amphibolis antarctica* and *Amphibolis griffithii* may establish itself on hard substrate with only a thin veneer of sediment which is frequently scoured.

Detritus accumulation rarely occurs, and the seagrass *Halophila australis* may occur in deep water environments due to good water clarity.

**Fig. 3.7** Seagrass habitats in southern Australia, from Spencer Gulf to the east

Australian waters have greater *Posidonia* species diversity than South Australia. The deeper waters of the South Australian coast are typically home to *P. sinuosa*, and *P. angustifolia* (and *A. antarctica* and *A. griffithii*) (Edyvane 1999).

In the inverse estuaries (large gulfs) of South Australia the tidal range is much greater (up to 3.6 m) than the microtidal tides typical of the region, and tides within the gulfs are typified by periods of minimal tidal movement (termed a 'dodge' tide) (*also see the Shark Bay text box for an example in Western Australia*). These waters are also hypersaline, with mean salinities of 42–49 ppt in North Spencer Gulf and 35–42 ppt in Gulf of St Vincent (Edyvane 1999). These conditions create sheltered intertidal seagrass habitats dominated by *Heterozostera*.[1] Enduring meadows of *Posidonia australis* dominate the sheltered subtidal areas, and in the deeper gulf waters, *P. sinuosa*, *P. angustifolia* and *A. antarctica* are common. *Posidonia ostenfeldii* complex can form small communities in more exposed waters and *Halophila australis* has been found as deep as 23 m in offshore gulf waters (Edyvane 1999).

Estuarine waters are home to just a few of the seagrasses found in the region, likely due fewer species being tolerant to the frequent large swings in salinity. In the south-west estuaries with permanent connections to the ocean, monospecific meadows of *Halophila ovalis* usually dominate. In these estuaries, *Halophila decipiens* can co-occur with *H. ovalis* or occur by itself (Kuo and Kirkman 1995). *Zostera muelleri* tends to be found close to the mouth of the estuary, where salinity is more marine and fluctuates less. Interestingly, *Posidonia australis* has recently

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[1] Note historical reports of *Zostera tasmanica* e.g. Edyvane (1999), have been interpreted as *Heterozostera nigricaulis*, based on Kuo (2005).

been observed in the Swan-Canning estuary (M. Sanchez-Alarcon, V. Forbes pers. comm, 15 Dec 2015) associated with reduced rainfall and streamflow in the catchment (Petrone et al. 2010; Silberstein et al. 2012). *Ruppia megacarpa* is the most common seagrass in the occasionally open bar-built estuaries of the south-coast, such as Wilson Inlet (Carruthers et al. 1999, 2007). *Posidiona australis*, *P. sinuosa*, *Amphibolis antarctica* and *A. griffithii* can be found in a few of the permanently open estuaries on the south-coast, such as Oyster Harbour and Waychinicup, where large connections to the ocean ensure good marine water exchange. Hydrological modifications and water abstraction from the River Murray has altered the seagrass ecology of the Coorong in South Australia and resulted in the substantial reduction in area of both *Ruppia megacarpa* and *Ruppia tuberosa* (McKirdy et al. 2010; Whipp 2010; Dick et al. 2011).

Geomorphological differences between the south-west of Western Australia and south coast of Western Australia and South Australia create a range of different seagrass habitats. Exposure is thought to be a key factor influencing not only what seagrasses can prevail, and may also be a proxy for other ecological aspects. For example, the genetic diversity of *Posidonia australis* is greater in more open waters than inshore sites which have low water movement and/or face strong prevailing winds at the time of seed dispersal (Sinclair et al. 2014). Light and nutrient availability also influence seagrass habitats in this region (Cambridge and Hocking 1997; Collier et al. 2007; Lee et al. 2007; Ralph et al. 2007).

Hydrodynamic conditions are a significant driver of seagrass habitats across multiple scales. At the largest of these scales, the Leeuwin Current system (including the Capes Current and Creswell Currents) and Flinders Current provide dispersal and connectivity opportunities for seagrasses in this region. For example, floating fruit of *Posidonia australis*, moved by either currents or local winds, has the potential to regularly connect meadows 10s of kilometres apart, and occasionally connect meadows 100s of kilometres apart (Ruiz-Montoya et al. 2015). This effect is species dependent however, as the different fruiting and seed strategy and morphology alter their dispersal modes and capabilities (Ruiz-Montoya et al. 2012).

The two large gulfs of South Australia, Gulf St Vincent (6,800 km$^2$) and Spencer Gulf (ca. 22,000 km$^2$), are often categorised as inverse estuaries (Kämpf 2014). The large scale water movements into and out of these systems are strongly seasonal (Middleton et al. 2013; O'Connell et al. 2016). Within Spencer Gulf, where the most detailed analysis of water movement has been conducted (Middleton et al. 2013), essentially water movement remains within the gulf during the summer months with a nearshore northward water movement pattern. The winter pattern of current movement in Spencer Gulf leads to exchange with the oceanic waters outside the gulf and there is a stronger mixing across the gulf, east to west. As a result, during the warmer summer months, the period of propagules dispersal for many species especially *Posidonia*, a higher proportion of floating seeds would be retained within the system. In cooler months, the movement of *Amphibolis* seedlings occurs and these would be able to be transported further within and outside the Spencer Gulf system.

At the meadow scale, hydrodynamics affects the species of seagrass found within each habitat type. Seagrasses exposed to strong ocean swells (such as the southwest coast of Australia), appear to have adaptations to allow them to cope with significant drag forces (de los Santos et al. 2012, 2016). Both *Amphibolis griffithii* and *Amphibolis antarctica* meadows effectively baffle water flow, and *A. antarctica has* been shown to reduce water flows from 50 to 2–5 cm $s^{-1}$ (Verduin and Backhaus 2000). Additionally, the wiry stems of these species may provide further protection from strong water movement. Similarly, *P. ostenfeldii* group of species typically form patchy meadows with mixed species in open-ocean or rough water (Campey et al. 2000). They are characterised by their long, thick, leathery leaves and long leaf sheaths that are deeply buried, and vertical rhizome growth. These characteristics appear to be associated with strong wave energy as well as highly mobile sand substratum, typical of the environments in which the *P. ostenfeldii* seagrasses are found (Kuo and Cambridge 1984).

Marine waters in southern and south-western Australia are considered oligotrophic, with nitrate concentrations <1 μM (Pearce and Pattiaratchi 1999; Balzano et al. 2015). In addition, carbonate sediment prevalent through much of the region, adsorbs phosphate onto calcium carbonate particles (McGlathery et al. 1994). These low nutrient waters tend to result in water with high clarity, allowing light to penetrate deeply. Seagrasses in this region are commonly found in waters greater than 30 m deep, and sometimes significantly deeper (see information box *Deepwater Seagrass in Temperate Southern Waters*).

With such low nutrient concentrations in the overlying water, the abundance of dense, highly productive seagrasses in this region has seemed paradoxical. How nutrient availability might influence seagrass habitats has been explored in the south-western Australian region over recent decades. For example: nutrient concentrations differed for *Posidonia coriacea* and *Heterozostera tasmanica* growing on the same carbonate sediments in Success Bank (Walker et al. 2004), suggesting species-specific differences in the nutrient requirements or the strategy of nutrient uptake and reallocation. Both Cambridge and Hocking (1997) and Collier et al. (2010) demonstrated that nutrient reabsorption and translocation from older plant tissues contributed to the nutrient requirement for *Posidonia sinuosa* and *Posidonia australis*. The addition of N+P to a *P. australis* meadow at Rottnest Island did not enhance growth, shoot density or biomass within 4 months of fertilization (Udy and Dennison 1999), while fertilization (N, N+P, P and Fe-EDTA) had mixed results that appeared site specific for transplanted seagrass shoots of *Posidonia australis* in the Albany Harbours (Cambridge and Kendrick 2009). We now know that rather than seagrass growth being highly constrained by the low nutrient waters, seagrasses in these regions contribute significant carbon (and nutrients) across ecosystem boundaries (Hyndes et al. 2014). Seagrass wrack is deposited at high rates on temperate south and south-western beaches (Kirkman and Kendrick 1997), and this wrack supports detrital consumers in both terrestrial and marine ecosystems (Ince et al. 2007; Heck et al. 2008). This detrital cycle seems highly important for the ecoregion.

**Table 3.2** Range in depths where seagrasses have been observed or collected from Western and South Australia

| Species | Depth range (m) | Reference |
|---|---|---|
| *Halophila ovalis* | 0.1–38 | Hillman et al (1995)<br>Huisman et al. (1999) |
| *Heterozostera nigricaulis* | 0.5–16.9 | Kuo (2005) |
| *Heterozostera polychlamys* | 2–48 | Kuo (2005) |
| *Posidonia australis* | 0.1–15 | Cambridge and Kuo (1979) |
| *Posidonia sinuosa* | 0.1–15 | Cambridge and Kuo (1979) |
| *Posidonia angustifolia* | 2–44 | Cambridge and Kuo (1979)<br>Huisman et al. (1999) |
| *Posidonia ostenfeldii* | 5–20 | Kuo and Cambridge (1984) |
| *Posidonia coriacea* | 1–30 | Kuo and Cambridge (1984) |
| *Posidonia denhartogii* | 1–10 | Kuo and Cambridge (1984) |
| *Posidonia robertsoniae* | 0.5–20 | Kuo and Cambridge (1984) |
| *Posidonia kirkmanii* | 6–18 | Kuo and Cambridge (1984) |
| *Amphibolis antarctica* | 0.1–27.3 | Walker and McComb (1988), Shepherd and Womersley (1981) |
| *Amphibolis griffithii* | 0.5–44 | Shepherd and Womersley (1981)<br>Huisman et al. (1999) |
| *Thalassodendron pachyrhizum* | 2–48 m | Kirkman and Cook (1987)<br>Huisman et al. (1999) |

### Information Box: Deepwater Seagrasses in Temperate Southern Waters

Seagrasses have wide depth distributions in south and south-western Australia, and extreme depth records occur in very clear oceanic waters with low light attenuation on the continental shelf of temperate Australia (Duarte 1991; Gattuso et al. 2006). These deep-water seagrass communities are heavily influenced by availability of hard substrata (to anchor within) and by significant wave height and benthic shear from ocean swells and currents (Hemer 2006).

A survey of the taxonomic and distribution literature (Table 3.2) indicates that most species found in temperate Australia have been reported from a broad range of depths. The *Posidonia australis* complex is generally found in sheltered bays and estuaries with species that are predominantly sheltered and shallow water (<15 m) in distribution (*P. australis*) and species that are predominantly exposed coastal and offshore deep water adapted (*P. angustifolia*) (Cambridge and Kuo 1979). The *P. ostenfeldii* complex are predominantly all deepwater species with distributions well beyond 15 m and restricted in distribution to sheltered bays to open ocean environments (Kuo and Cambridge 1984). *Heterozostera*, *Amphibolis* and *Halophila* species are found in sheltered estuarine and coastal environments but occur in the open ocean to 40 + m depths (Shepherd and Womersley 1981; Shepherd and Robertson 1989). *Thalassodendron pachyrhizum* is predominantly a deep-water species but can be found in shallow waters where benthic shear from swells is high. It has been reported to form extensive meadows at 35 m and greater depths (Kirkman and Cook 1987). Our knowledge of temperate deepwater seagrass communities is restricted to broad habitat information and occurrence and little research has characterised seagrass distributions and seagrass adaptation to deeper, more wave exposed environments.

Recent remote surveys using video and hydroacoustic methods have expanded our knowledge of distribution and in this section we will present data about seagrass distribution from Recherche Archipelago from extensive video tows. Also we will propose that *T. pachyrhizum* is a deepwater seagrass and present data from drop video surveys of Cape Naturaliste, as well as deeper and remote continental shelf environments west of Jurien, Western Australia.

The inshore continental shelf near Esperance, Western Australia encompassing the western Recherche Archipelago from Figure of Eight to Mondrain Islands, was recently mapped (Kendrick et al. 2005) and one of the major surprises was that seagrasses were not restricted to sheltered inshore environments but found subtidally near islands greater than 30 km offshore and at depths to 50–60 m. An extensive database allowed for the depth distribution of major seagrass genera to be determined (Fig. 3.8). For the genus *Posidonia* the average depth across all 7 species observed was 16.7 ± 7.4 m (mean ± SD, n = 692) and a maximum recorded depth of 37 m. For the genus *Amphibolis* (*A. antarctica* [rock] and *A. griffithii* [sand]), the average depth was 19.9 ± 8.9 (mean ± SD, n = 175) and a maximum recorded depth of 51 m. For the genus *Halophila* (predominantly *H. ovalis* and *H. australis*) the average depth was 22.4 ± 8.3 (mean ± SD, n = 282) and a maximum recorded depth of 49 m. The average depth for all genera are greater than the criteria used to define deep-water seagrass communities in tropical Australia (Coles et al. 2009) where only *Halophila* species are present deeper than 15 m. The diverse mix of temperate seagrass species found at depth in the waters of Esperance demonstrates the link between water clarity and seagrass depth distributions as originally summarized by Duarte (1991) and later modelled by Gattuso et al. (2006).

*Thalassodendron pachyrhizum* is a species that occurs predominatly in deeper waters on the continental shelf or wave swept shallower waters nearer the coast. Preliminary research on leaf production, biomass, reproduction and the production of viviparous seedlings indicates it is well adapted to deeper low light, high wave energy mid- to outer continental shelf environments (Kirkman and Cook 1987; Kuo and Kirkman 1987). Drop camera surveys were undertaken at Cape Naturaliste across depths from 15 to 60 m and at the

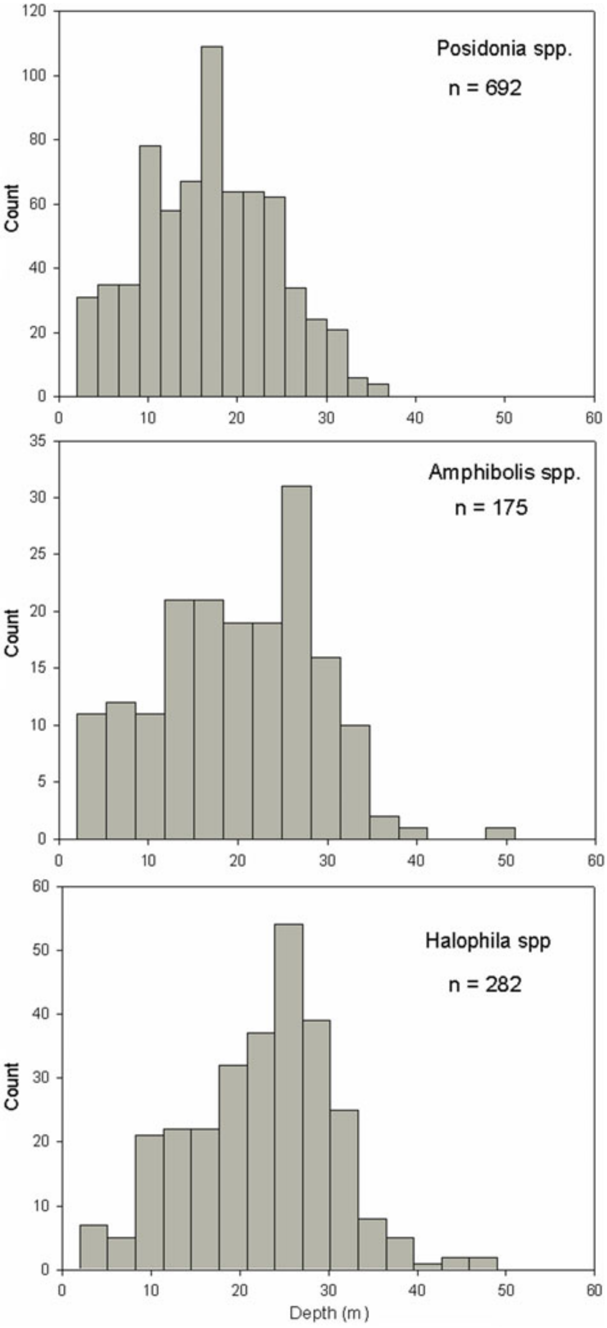

**Fig. 3.8** Frequency histograms of depth distribution of major genera of seagrass found in the western Recherche Archipelago (Data from Kendrick et al. 2005)

edge of the continental shelf >30 km west of Jurien Bay in 25–70 m depth, during 2008 as part of a National Heritage Trust II project 'Securing WA's marine futures' (Radford et al. 2008). Surveys on limestone and granite reefs at Cape Naturaliste found the average depth where *T. pachyrhizum* occurred was 33.8 ± 5 m (mean ± SD, n = 55) with a maximum recorded depth of 43.5 m. Surveys on the limestone reefs at the edge of the continental shelf found the average depth where *T. pachyrhizum* occurred was 35.3 ± 3.5 m (mean ± SD, n = 140) with a maximum recorded depth of 49 m. The survey extents were 166 $km^2$ for Cape Naturaliste and 72 $km^2$ for Jurien. The coverage of seagrasses was patchy but extensive, suggesting these meadows are ubiquitous across these depths on sand covered limestone reef and pavement on mid to outer shelf oceanic environments. Their role and importance in the deep shelf environments is presently unknown. Similar deepwater collections have been made for many of the seagrasses in southern Australia indicating deepwater seagrass meadows are ubiquitous although patchy in distribution across much of the continental shelfs of temperate Australia.

## 3.4 Impacts on Seagrasses in this Region

The major threats to seagrasses are coastal development, eutrophication, extreme climate events and global warming. Over the last two decades, the loss of seagrass from direct and indirect human impacts amounts to 18% of the documented global seagrass area (Green and Short 2003).

In Western Australia, significant areas of seagrass have been lost in protected coastal embayments (Table 3.3). The most well documented anthropogenic loss of 1000s of hectares of seagrass is Cockburn Sound. In the 1950s and 1960s, the seagrass species *Posidonia sinuosa*, *P. angustifolia* and *P. australis* formed an almost continuous meadow between 1 and 10 m depth that fringed the eastern, southern and western coasts of the sound. Over 5 years, between 1967 and 1972, 1587 ha of seagrass meadows were lost from the eastern and south-eastern shallow shelfs (<10 m depths) of the Sound (Cambridge and McComb 1984). The decline in area of seagrass cover was driven by nutrient inputs from sewage, a fertiliser plant and other industrial effluents (Cambridge et al. 1986; Kendrick et al. 2000, 2002). The significant quantity of dead seagrass leaf and rhizome material that entered detrital pathways from the seagrass loss (Cambridge and Hocking 1997), over extensive areas of the eastern and southern fringing shelves fuelled the conversion of the inshore ecosystem from net autotrophic to net heterotrophic. Losses of seagrasses continued into the 1980s and early 1990s. Loss through dredging and land reclamation has also occurred in Cockburn Sound, Albany harbours and Esperance Bay, but the scale of direct impact is in the 10s to 100s of ha (Table 3.3).

**Table 3.3** Drivers of seagrass decline and scale of seagrass response in the SW of Australia

| Authors | Location | Spatial extent | Driver | Response |
|---|---|---|---|---|
| Hastings et al. (1995) | Rottnest Island, Western Australia | 81 ha | Mooring and anchoring of boats | Rocky Bay loss of seagrasses total 31%<br>18% 1941–1981<br>13% 1981–1992<br>Thomson Bay<br>1941–92 < 5%<br>Fragmentation occurring but seagrass recovery fast |
| Kendrick et al. (2000) | Success and Parmelia Banks, West. Australia | 3,974 ha | Channel dredging, limesands dredging, nutrients | Between 1965 and 1995 there was a 21% increase in seagrass cover on Success Bank. On Parmelia Bank % cover of seagrasses has remained constant at approx 45%<br>Seagrasses responsible for gains are *Amphibolis griffithii* and *Posidonia coriacea* |
| Seddon et al. (2000) | Spencer Gulf, South Australia | 8,269 ha | Extreme low tide and warming of nearshore waters | Historical dieback between 1987 and 1994 in the intertidal and shallow subtidal<br>Over 8269 ha showed dieback attributed to climate change associated with El Niño |
| Kendrick et al. (2002) | Cockburn sound, Western Australia | 3,667 ha | Eutrophication | Historical decline in seagrass area by 77% since 1967. 1967–72: 1587 ha lost. 1972:1981: 602 ha lost. 1981–1999: 79 ha lost. Species of seagrass lost were predominantly *Posidonia sinuosa* |
| Bryars et al. (2003), Bryars and Neverauskas (2004) | Adelaide waters, South Australia | 365 ha | Nutrients, smothering and reduced light | Loss of seagrass in area near sewage outfall. Recovery was slow and dominated by *Halophila australis* |
| Hegge and Kendrick (2005) | Esperance Bay | 773 ha | Port infrastructure, dredging and land reclamation | Between 1956 and 2001 83 ha were reclaimed, 72 ha were dredged resulting in in the loss of 116 ha of predominantly *Posidonia sinuosa* meadows |
| Bryars and Rowling (2009) | Eastern Gulf of St Vincent | >2,000 ha | Wastewater treatment plant outfalls (and thus elevated nutrients) | Selective disappearance of *Amphibolis* in three distinct areas since the 1930s, with loss in one area (Henley Beach to Brighton) estimated to be 1,000–2,000 ha |

Indirect impacts from dredging have only recently been addressed (Fraser et al. 2017) and the extent of combined indirect and direct effects is generally underestimated. Mooring and anchor damage has also been reported at Rottnest Island near Perth with combined losses from many mooring in the range of 10s of hectares, predominantly driven by physical scouring of the bottom by chains. The largest recent losses of seagrasses in Western Australia were driven by a marine heatwave in 2011 (1,000s of km$^2$: see information box *Climate Change—increases in extreme events*) and subsequent synergistic interactions, with light availability from floods and increased turbidity associated with microbial breakdown of seagrass biomass, that continued to drive seagrass loss for over 2 years.

In South Australia, most reported loss of seagrass meadows has been linked to increased nutrient inputs and subsequent synergistic interactions with associated sediment destabilisation. Approximately 5,000 ha of seagrasses were lost over 70 years from the metropolitan Adelaide coastline in eastern Gulf St Vincent. The initial loss was linked to wastewater treatment plant outfalls and stormwater discharges, and subsequent loss associated with increased sediment mobilisation and local erosion (Westphalen et al. 2004). Approximately 168 ha of seagrass were lost near Port Lincoln in southwestern Spencer Gulf due to declining water quality including discharge wastes from fish processing factories (Hart 1999; Gayland 2009). Similarly, significant losses of subtidal seagrasses reported in Western Cove on Kangaroo Island were linked to eutrophication due to land-based nutrient inputs (Bryars et al. 2003), as was the disappearance of large areas of deepwater *Heterozostera* over a 30-year period in Investigator Strait/Gulf St Vincent, where losses may have been due to land-based discharges and prawn trawling (Tanner 2005). Also, other activities reported to have impacted seagrasses include mining and seismic operations, construction works, aquaculture structures, and moorings (Shepherd et al. 1989; Madigan et al. 2000; Bryars 2003; Bryars et al. 2003). Large-scale natural losses of intertidal and shallow subtidal seagrasses (up to 13,000 ha) in northern Spencer Gulf were linked to extreme weather conditions (Seddon et al. 2000). The spatial scale of loss from climate and oceanographic events like the Spencer Gulf and Shark Bay examples described here are generally much greater (1,000s of ha to 1,000s of km$^2$) than those associated with direct anthropogenic impacts, and the combined impacts from multiple stressors at the ecosystem scale, like those in Cockburn Sound and Adelaide waters pose the greatest threat to temperate seagrasses in in western and southern Australia.

### Information Box: Climate Change—Increases in Extreme Events

#### *Shark Bay Seagrass Defoliation—Marine Heatwave of 2011*

In summer 2011, the west coast of Australia was affected by a marine heat wave that elevated sea temperatures 2–4 °C higher than normal over several weeks, resulting in coral bleaching, macroalgal mortalities, and fish kills over much of the coast (Wernberg et al. 2013). In Shark Bay, temperate species, *Amphibolis antarctica* and *Posidonia australis* are the dominant seagrasses, although they are towards the northern limits of their geographical distribution. Tropical species of the genera *Cymodocea*, *Halodule* and *Halophila* are found growing with these temperate species.

Defoliation of *A. antarctica* meadows was observed baywide but was more extreme in areas of high turbidity, driven either by detrital pools across the whole Shark Bay System as well as riverine particulates in floodwaters from the Wooramel River. *A. antarctica* was susceptible to decreases in light availability when combined with higher temperatures, presumably due to increased respiratory demand with no ability to increase photosynthesis to match (Walker and Cambridge 1995). The small, tropical seagrass species, *H. uninervis* was unaffected by the combined flooding and warming event as it is adapted to higher water temperatures. In addition, high seed production and dormancy in the sediments in this seagrass would be well suited to increases in frequency and intensity of disturbance events like marine heatwaves and riverine flooding.

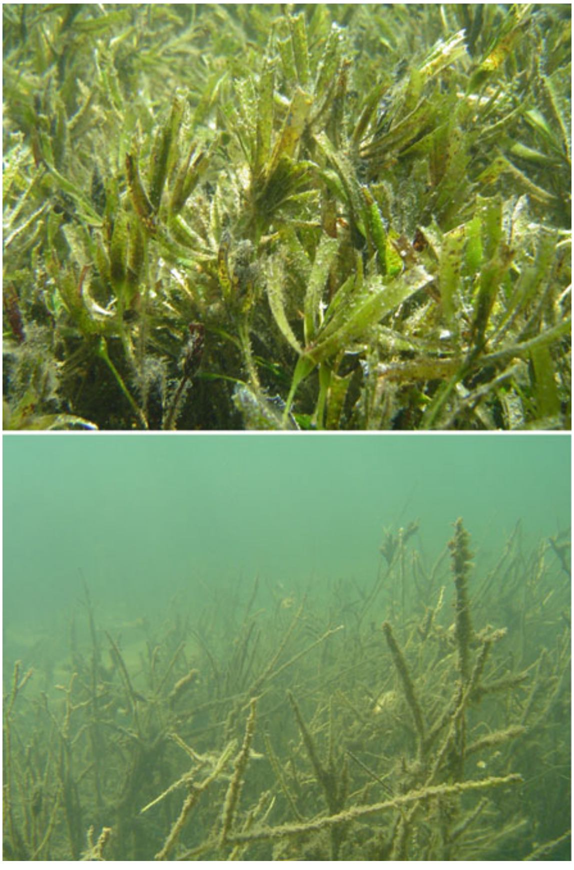

**Fig. 3.9** Healthy meadows of *Amphibolis antarctica* in Shark Bay (top) and defoliated meadow after 2011 marine heatwave (bottom) on the Wooramel Bank, Shark Bay Western Australia

In the eastern gulf, defoliation of *Amphibolis antarctica* increased with proximity to floodwaters originating from the Wooramel Delta (Fraser et al. 2014). In March, two months after the combined effects of high water temperatures generated by the marine heatwave 2011 and flooding from extreme weather, plants were either totally or showed a high level of defoliation within 15 km of the Wooramel river mouth (Fig. 3.9) and plants subsequently died. Above-ground (leaf) biomass 2 years later was only 7–20% of that recorded before the 2011 marine heatwave.

Similarly, in the L'Haridon Bight, Monkey Mia and Peron Peninsula meadows, wide-scale defoliation of *A. antarctica* and death of meadows was clearly observed 1 year after the marine heatwave. Percent cover of *A. antarctica* declined from median values of 65% to less than 10% in L'Haridon Bight (31 sites), 80% to <10% in sites at Monkey Mia (42 sites), 65% to <5% on the eastern Peron Peninsula (20 sites), and 65–25% on the eastern Peron Peninsula including Denham (20 sites) (Thomson et al. 2015).

Defoliation of *A. antarctica* was a bay-wide phenomenon. The greatest effects were seen in shallow areas nearshore, at depth, and in turbid waters. The loss of a major foundation species across such a wide region in Shark Bay has already affected seagrass dependent marine organisms with a decline in health status of the herbivorous green sea turtle, *Chelonia mydas*, evidence that there were long-term community-level impacts to Shark Bay from the marine heatwave (Thomson et al. 2015).

The other major seagrass, *Posidonia australis* did not show defoliation across the bay, but 100% seed abortion was observed from flowering in the Western Bay and Peron Peninsular (Sinclair et al. 2016). Flowers developed pericarp (fruit) but these were all empty, containing aborted embryos. Successful reproduction has only recently been observed in 2016.

Given the ecological importance of *A. antarctica* in Shark Bay, accounting for 85% ( $\sim$3700 $km^2$) of the total cover of seagrasses (Walker et al. 1988), predicted increases in the frequency and magnitude of marine heat waves and floods will have catastrophic implications for these seagrass ecosystems at the northern extremes of their distribution. Also, a recent assessment of tropicalisation of temperate and tropical seagrasses ecosystems along the Western Australian coastline predicted that the temperate seagrasses *A. antarctica* and *P. australis* would contract in geographical distribution southward between 200 and 400 km by 2100 (Hyndes et al. 2016). Although this range contraction prediction is limited as it based only on published physiological optima and limits in temperature for these seagrasses, and thus did not take into account acclimation and adaptation to higher temperatures in these species, it does give a dire early warning of the future for temperate seagrasses that are already at their range limits.

## 3.5 Emerging Threats and Management Issues

With coastal development, eutrophication, extreme climate events and global warming, seagrasses in this region face a future of risk from multiple stressors at the ecosystem scale. The anthropogenic threats which have been responsible for many of the reported cases of localised seagrass loss are shown in Table 3.3. We expect increased human development of the coastal zone and associated effects of overfishing, physical destruction, and seagrass loss from eutrophication, increased turbidity, and other pollutants to continue to be a risk to seagrass in this region, however it is now combined with climate-related changes which have the potential to affect very large areas. Seagrasses exposed at low tide may be threatened by climate change (c.f. Seddon et al. 2000) and sea-level rises, particularly if hardening of coastlines occurs to protect infrastructure. Climate change also will bring changes in the frequency, seasonal timing and severity of storms and storm surges that threaten to physically remove seagrasses from shallow subtidal coastal areas. Estuarine seagrasses may be lost in some areas due to reductions in freshwater flows associated with climate change. Subsequent increases in salinities associated with evaporation in some shallow systems may be beyond the physiological tolerances of seagrasses (as already observed in The Coorong).

Invasive pest species, including *Caulerpa taxifolia* and *C. racemosa* that are already established in the Port River region of eastern Gulf St Vincent, South Australia, and may threaten seagrasses as documented in other parts of the world (De Villèle and Verlaque 1995). *C. racemosa* has also been observed within seagrass beds in the Leschenault Estuary, Western Australia (Department of Water and Environmental Regulation, unpublished data).

Disturbance of the natural hydrological and detrital cycles, through coastal development and construction of marinas, has been a realised management issue in the last decade in Western Australia. The highly productive seagrass meadows of Geographe Bay, and the annual detritus they produce, caused a significant management issue following the construction of Port Geographe. Breakwaters which were designed to prevent sand bar formation at the harbour entrance, actually became a very efficient trap of seagrass wrack (estimates of 100,000 $m^3$, several metres high and 1–2 km in length) (Pattiaratchi et al. 2015). Loss of beach access and hydrogen sulfide generated from decaying seagrass wrack caused issues for local residents. The breakwater, seawall and entrance channel were eventually reconfigured at a cost of $28 million in 2015 to address the problem caused by the initial development (http://www.transport.wa.gov.au/portgeographe).

## 3.6 Summary

The southern and southwestern Australian marine environment is a region of unique biodiversity. The future of seagrasses in this region depends more than ever on smart and effective management preventing the impacts of major and emerging threats. Other than the loss of seagrass due to coastal development, the greatest threat to temperate seagrasses of this region is from climate and oceanographic events, such as heat waves. Indeed these climate associated losses occur at spatial scales that surpass those of the direct anthropogenic impacts. However, the future for effective management of seagrass is also brighter than ever, with increased understanding of recruitment bottlenecks, restoration options and aspects of seagrass resilience.

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# Part II
# Taxonomy and Anatomy

# Chapter 4
# Anatomy and Structure of Australian Seagrasses

**J. Kuo, M. L. Cambridge and H. Kirkman**

**Abstract** Seagrasses are monocotyledonous angiosperms, and as with terrestrial angiosperms, they have vegetative organs (roots, rhizomes and shoots with leaf sheaths and leaf blades), and reproductive organs (flowers, fruits and seeds). They have adapted to a marine environment in a saline medium, and have rather simple tissues and cell types such as a thin cuticle and epidermal cells with concentrated chloroplasts but lack stomata in the leaves. Within the vascular bundles, the cell walls of vascular bundle sheath cells are either lignified, suberized or have wall ingrowths. The number and size of xylem elements are much reduced in seagrasses. Phloem cells have thin or nacreous wall and/or thick walled sieve elements. Whether these structural variations are significant in solute translocation remains to be determined. Seagrass rhizomes are usually herbaceous, but some become woody. They are either monopodially or sympodially branched, with adventitious roots. Roots may be branched and bear roots hairs, depending on the substratum. Air lacunae are continuous within all vegetative and reproductive organs, with regular septa interrupting the air lacunae. Unusual apoplastic fungal hyphae grow in the intercellular spaces of living leaf tissue of the subtidal *Zostera muelleri*. Seagrasses are monoecious or dioecious plants with hydrophilous pollination. They have unusual filamentous pollen or pollen grains that form long chains. Fruits and seeds have either a period of dormancy or germinate as they are being released. Unlike seeds of other seagrasses, the embryos of *Amphibolis* and *Thalassodendron* do not store starch but instead obtain nutrients required for the prolonged devel-

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opment phase of the viviparous seedlings directly from the parent plant through ‘transfer cells’. Morphological and anatomical organization of both vegetative and reproductive organs vary among Australian seagrass taxonomic groups, reflecting their different evolutionary origins, as well as providing a means of indentifying genera and species with classical taxonomy.

## 4.1 Introduction

Seagrasses are monocotyledonous angiosperms, with general morphological structures and anatomical tissues similar to those in all flowering plant species; distinctive above (leaf and stem) and below ground (rhizome and roots) vegetative organs, and reproductive organs, in the form of flowers, fruits and seeds. However, unlike their terrestrial cousins, seagrasses grow and survive in seawater environments. Arber (1920) formulated a set of four properties for seagrasses (1) the plants must be adapted to life in a saline medium; (2) the plants must be able to grow when fully submerged; (3) the plants must have a secure anchoring system, and (4) the plants must have a hydrophilous pollination mechanism.

General vegetative morphology and anatomy of seagrasses were described and illustrated in the series of papers by Sauvageau (1889–1891) and recently reviewed and redescribed by Tomlinson (1982). The first published ultrastructure on Australian seagrasses was the leaf epidermis of *Cymodocea serrulata*, *C. rotundata* and *Thalassia hemprichii* from the Great Barrier Reef (Doohan and Newcomb 1976). Birch (1981) described the unusual seedling development on *Halophila spinulosa* from Queensland. Ducker and her team (McConchie, Pettitt, Knox, see references) made a very important contribution on submarine pollination with fine structure of seagrass pollen and anatomy and reproduction of *Amphibolis* and *Posidonia*. Kuo and co-researchers (see references) provided vegetative and reproductive anatomy and ultrastructure of many Australian species over the last twenty years. Barnabas (1983–1996) also contributed vegetative ultrastructural studies on several South African seagrasses, some of which also occur in Australian waters, such as *Thalassodendron ciliatum* and *Halodule uninervis*. This chapter reviews morphology, anatomy, and ultrastructure and reproductive biology of the Australian seagrasses; the subject had been dealt with previously (Kuo 1983a; Kuo and McComb 1989; Kuo and den Hartog 2006).

## 4.2 Plant External Morphology (See also Table 4.1)

Seagrasses generally have a similar external morphology with a well-developed creeping rhizome. At rhizome nodes, there is either a foliage leaf as in *Posidonia*, *Zostera* (Fig. 4.1e) or a short or long erect shoot bearing several foliage leaves, each with a sheath at the base as in *Cymodocea*, *Amphibolis* (Fig. 4.1a) and

**Table 4.1** Some vegetative features of australian seagrasses

| | Leaf | Rhizome | | | | Root | | |
|---|---|---|---|---|---|---|---|---|
| | | Hardness | Stem | Axes | Branching | Root no. at rhizome node[a] | Branching | Root hairs |
| *Enhalus* | Flat, linear | Herbaceous | Absent | Monomorphic | Monopodial | Few | Unbranched | Infrequent |
| *Thalassia* | Flat, linear | Herbaceous | Present | Dimorphic | Monopodial | 1 | Unbranched | Numerous |
| *Halophila* | Flat, oval to oblong | Herbaceous | Absent or present | Mono/ dimorphic | Sympodial | 1 | Unbranched | Numerous |
| *Posidonia* | Terete to flat, linear | Herbaceous | Absent | Monomorphic | Monopodial | 2–3 | Branched | Infrequent |
| *Cymodocea* | Flat, linear | Herbaceous | Present | Dimorphic | Monopodial | 1–5 | Branched | Infrequent |
| *Halodule* | Flat, linear | Herbaceous | Present | Dimorphic | Monopodial | 1 or more | Unbranched | Numerous |
| *Syringodium* | Terete, linear | Herbaceous | Present | Dimorphic | Monopodial | 1 or more | Branched | Numerous |
| *Amphibolis* | Flat, short | Woody | Present | Dimorphic | Sympodial | 1–2 | Branched | Infrequent |
| *Thalassodendron* | Flat, linear | Woody | Present | Dimorphic | Sympodial | 1–5 | Branched | Infrequent |
| *Zostera* | Flat, linear | Herbaceous | Absent | Monomorphic | Sympodial | 2 or more | Branched | Numerous |
| *Heterozostera* | Flat, linear | Herbaceous | Absent or present | Mono/ dimorphic | Sympodial | 2 | Branched | Numerous |

[a] Roots are not produced at each rhizome nodes of certain genera, i.e. *Thalassia*, *Thalassodendron*, *Amphibolis* etc.

*Thalassodendron*. There are exceptions: each shoot of *Halophila* carries 2–3 petiolate leaves that do not have sheaths (Fig. 4.1f). In all seagrass species, one or more branched or unbranched roots are produced at the rhizome nodes (Fig. 4.1a, b, e, f).

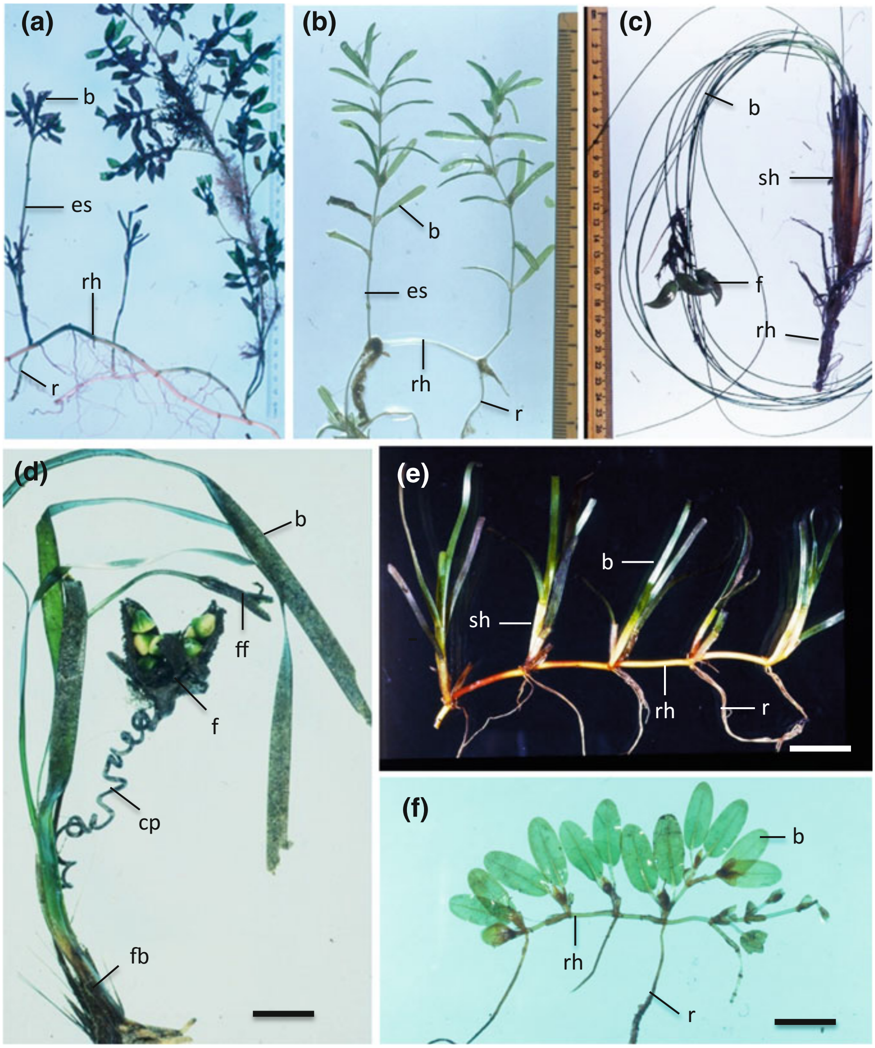


**Fig. 4.1** Plant morphology. **a** *Amphibolis antarctica*. **b** *Halophila tricostata*. **c** *Posidonia denhartogii*. **d** *Enhalus acoroides*, scale = 5 cm. **e** *Zostera capricorni*, scale = 1.5 cm. **f** *Halophila decipiens*, scale = 1.5 cm, b: leaf blade, cp: coiled peduncle, es: erected stem f: fruits, fb: fibre bundles, ff: female peduncle; r: roots; rh: rhizomes; sh: leaf sheath

## 4.3 The Foliage Leaf

The foliage leaf is produced either from the rhizome node in *Zostera* (Fig. 4.1e), *Heterozostera* (not *H. nigricaulis*), *Posidonia*, *Enhalus* and *Halophila* section Halophila, or from an erect stem apex in all genera in Cymodoceaceae (Fig. 4.1a), *Thalassia*, *Halophila spinulosa* and *H. tricostata* (Fig. 4.1b). The foliage usually forms a unit of several leaves, and normally is referred to as a shoot containing different developmental stages of leaves; the inner ones being the youngest. Each leaf consists of a basal leaf sheath and a distal leaf blade, these leaves usually are long linear, but *Amphibolis* has shorter leaves and *Syringodium* has terete leaves.

## 4.4 Leaf Blade (See also Table 4.2)

**Surface**: The leaf surfaces of seagrasses do not have stomata, as they grow in marine environments. Unicellular trichomes of various lengths may occur in *Halophila decipiens* and *H. capricorni* (Fig. 4.2i, j). Leaf blade margins, particular in the distal regions of *Thalassia*, *Thalassodendron*, *Cymodocea* and certain species of *Halophila* also bear short unicellular trichomes. Seagrass leaves have a similar adaxial and abaxial surface in cross sections, so sometimes it is not easy to determine the adaxial or abaxial surface in the section, but the xylem is always facing the upper (adaxial) surface of leaves.

## 4.5 Cuticle

There is always a very thin layer (<0.5 μm) of ‘cuticle’, covering the outer surface of epidermal cells. The appearance of the cuticle under electron microscopy differs among seagrass species; it appears as a 0.1–0.2 μm, electron transparent layer in *Halophila*, *Thalassodendron* and *Syringodium* (Fig. 4.5c); or 0.5 μm porous layer in *Thalassia*, *Posidonia* and *Amphibolis* (Fig. 4.5d); or an electron transparent layer 0.05 μm thick with ‘subcuticular cavities’ at the outer most tangential walls in *Enhalus*, *Zostera* (Fig. 4.5b) and *Heterozostera*, *Cymodocea* and *Halodule*. When exposed to the air during a low tide, the overlapping leaves rather than the thin cuticle provide some protection from desiccation (Clough and Attiwell 1980).

**Table 4.2** Leaf blade features of Australian seagrasses

| Genus | Cuticle | Epidermal cell wall | Fibre bundles | Air lacuna | Vascular bundle sheath | Sieve tubes walls thin or nacreous | Xylem |
|---|---|---|---|---|---|---|---|
| *Enhalus* | Porous | Normal | Present | Distinct | Normal | Thin walled | Tracheids/lacuna |
| *Thalassia* | Porous | Ingrowths | Present | Distinct | Normal | Thin walled | Tracheids/lacuna |
| *Halophila* | Transparent | Ingrowths | Absent | Not distinct | Normal | Nacreous walled | Tracheids/lacuna |
| *Posidonia* | Porous | Normal | Present | Distinct | Lignified | Thin walled | Tracheids/lacuna |
| *Cymodocea* | ‘Cavity’ | Ingrowths | Present | Distinct | Suberized | Thin walled | Tracheids/lacuna |
| *Halodule* | ‘Cavity’ | Ingrowths | Absent | Distinct | Normal | Nacreous walled | Tracheids/lacuna |
| *Syringodium* | Transparent | Normal | Absent | Distinct | Suberized | Thin and thick walled | Tracheids/lacuna |
| *Amphibolis* | Porous | Normal | Absent | Not distinct | Suberized | Thin walled | Tracheids/lacuna |
| *Thalassodendron* | Transparent | Ingrowths | Absent | Not distinct | Suberized | Thin and thick walled | singular/lacuna |
| *Zostera* | ‘Cavity’ | Ingrowths | Present | Distinct | Ingrowths | Nacreous walled | singular/lacuna |
| *Heterozostera* | ‘Cavity’ | Ingrowths | Present | Distinct | Ingrowths | Nacreous walled | singular/lacuna |

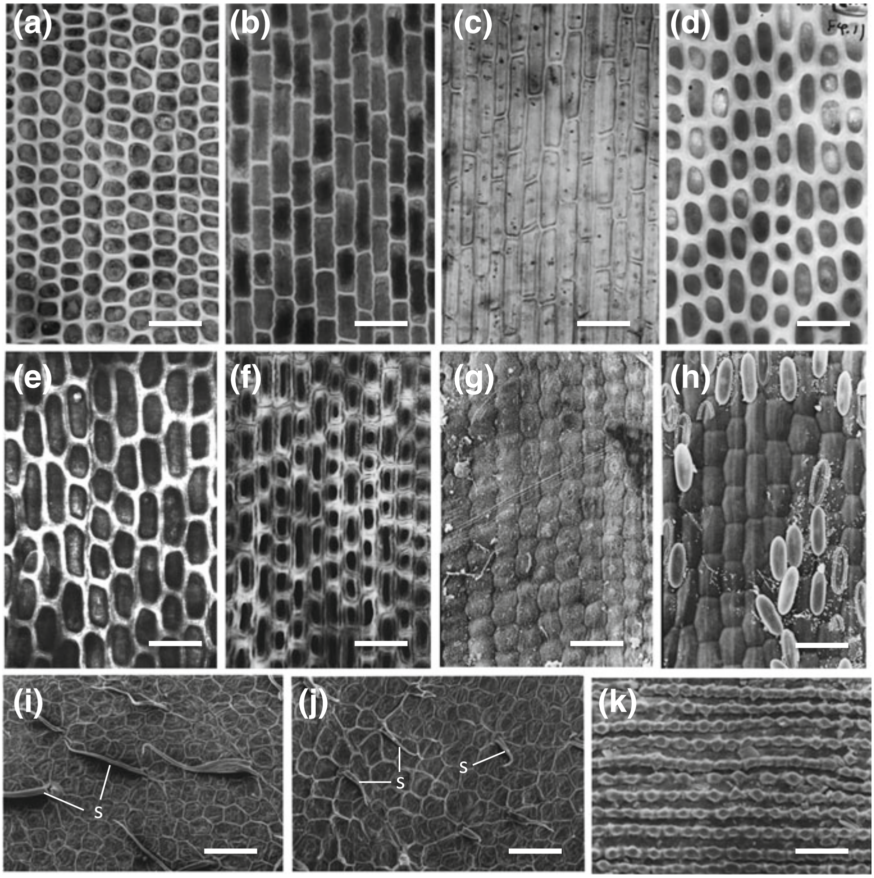
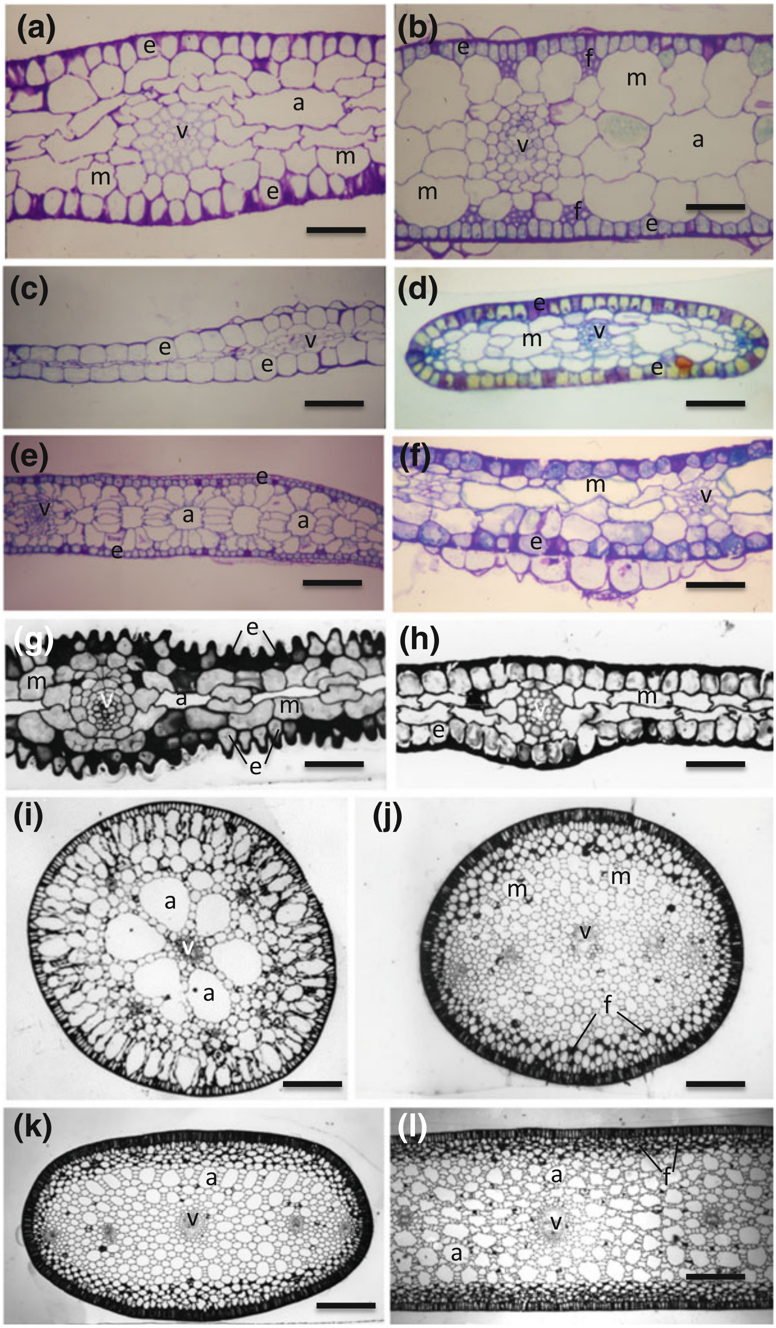


**Fig. 4.2** The LM surface view of the *Posidonia* leaf blade epidermis: **a** *Posidonia australis*. **b** *P. sinuosa*. **c** *P. angustifolia*. **d** *P. coriacea*. **e** *P. kirkmanii*. **f** *P. robertsonae*, scales = 20 µm. **g**–**k** SEM images of seagrass blade epidermis: **g** *Zostera capricorni*. **h** *Z. mucronata*, scales = 40 µm. **i** *Halophila capricorni* adaxial surface. **j** The abaxial surface of the same specimen, s: setae, scales = 20 µm. **k** *Heterozostera nigricaulis*. *Note* the colliculate outer surfaces of epidermal cells have unusual protruberances, scale = 30 µm

## 4.6 Epidermis

The morphology and structure of leaf epidermal cells are similar on both surfaces. The shape of the epidermis cells may differ between seagrass species either in surface or transverse sectional view, which sometimes serves as a useful taxonomic character, for example in *Posidonia* species (Fig. 4.2a–f). *Heterozostera nigricaulis* epidermal cells have an unusual colliculate outer surface (Kuo 2005; *see* also Figs. 4.2k, 4.3g), while the epidermis of all other *Zostera* species have a smooth outer surface (Figs. 4.2g, h and 4.3e). The walls of epidermal cells contain pectin, protein, and cellulose but no lignin (Ducker et al. 1977; Kuo 1978; Cambridge and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◂**Fig. 4.3** Internal organization of leaf blade in seagrasses. **a** *Amphibolis antarctica*, scale = 100 μm. **b** *Cymodocea serrulata*. **c** *Halophila spinulosa*, scale = 100 μm. **d** *Halodule piniforlia*, scale = 50 μm. **e** *Heterozostera polychlamys*, scale = 150 μm. **f** *Cymodocea serrulata*, scale = 80 μm. **g** *Heterozostera nigricaulis*, scale = 80 μm. **h** *Thalassodendron pachyrhizum*, scale = 80 μm. **i** *Syringodium isoetifolium*, scale = 200 μm. **j** *Posidonia ostenfeldii* (base) and **k** *P. ostenfeldii* (distal), scale = 170 μm **l** *Posidonia coriacea*, scale = 40 μm., a: air lacunae; e: epidermis; f: fibre bundles; m: mesophyll; v: vascular bundles. *Note* large air lacunae present in *Zostera* and *Syringodium*, while numerous fibrous bundles (f) occur in *Posidonia* spp., and an unusual epidermis in *H. nigricaulis*

Kuo 1982). Ultrastructurally, there are two distinct types of the blade epidermal cells: (a) Wall ingrowths and convoluted plasmalemma are absent in the blade epidermal cells of *Posidonia*, *Amphibolis* and *Syringodium* (Fig. 4.5c). (b) In other genera, the presence of wall ingrowths, characteristic of transfer cells, are associated with a convoluted plasmalemma with a relatively large inner surface area (Doohan and Newcomb 1976; Kuo 1983b). These peculiar ‘wall ingrowths’ are normally more pronounced on the inner than outer tangential wall (Fig. 4.5a) indicating that they may be related to solute transfer between epidermal and mesophyll cells (Kuo 1983a; Kuo et al. 1990).

The leaf blade epidermis is the major site of photosynthesis and the cells have concentrations of chloroplasts, mitochondria, lipid droplets, dictyosomes, endoplasmic reticulum and microbodies in most species (Fig. 4.5a, c). Furthermore, the blade epidermis may also contain polyphenolic substances (tannin) in vacuoles in all genera, except *Zostera* and *Heterozostera*. Comparative anatomical ultrastructural work on the Australian seagrasses has been reviewed (McComb et al. 1981; Kuo 1983a). The leaf anatomy of seagrasses does not conform closely to that of either $C_3$ or $C_4$ terrestrial plants.

## 4.7 Leaf Fibre Bundles

A fibre bundle usually consists of several fibre cells, which have thickened but not lignified walls with small lumens (Fig. 4.4a, b, e, f). The number of fibre cells per fibre bundle and their locations in a leaf blade have sometimes been used for the taxonomic identification of some genera, i.e., *Posidonia* and *Zostera*. In the family Zosteraceae, they are found in the hypodermis adjacent to air lacunae. In the *Posidonia australis* species group, which have flattened leaf blades, fibre bundles are present in the hypodermal and sub-hypodermal layers but absent from the mesophyll tissues. In contrast, the fibre bundles also extend into the mesophyll in the species with biconvex to terete blades, i.e. *P. ostenfeldii* species group (Figs. 4.3j–l).

Fibre bundles are only associated with the hypodermis adjacent to the longitudinal vascular bundles in the *Cymodocea* species, but they are absent in *Amphibolis*, *Halodule* (Fig. 4.3d), *Thalassodendron* (Fig. 4.3h), and *Syringodium* (Fig. 4.3i). They are associated with vascular bundles in *Enhalus*, also with the hyperdermis in *Thalassia*, but totally absent in *Halophila* (Fig. 4.3c). The fibre bundles and the

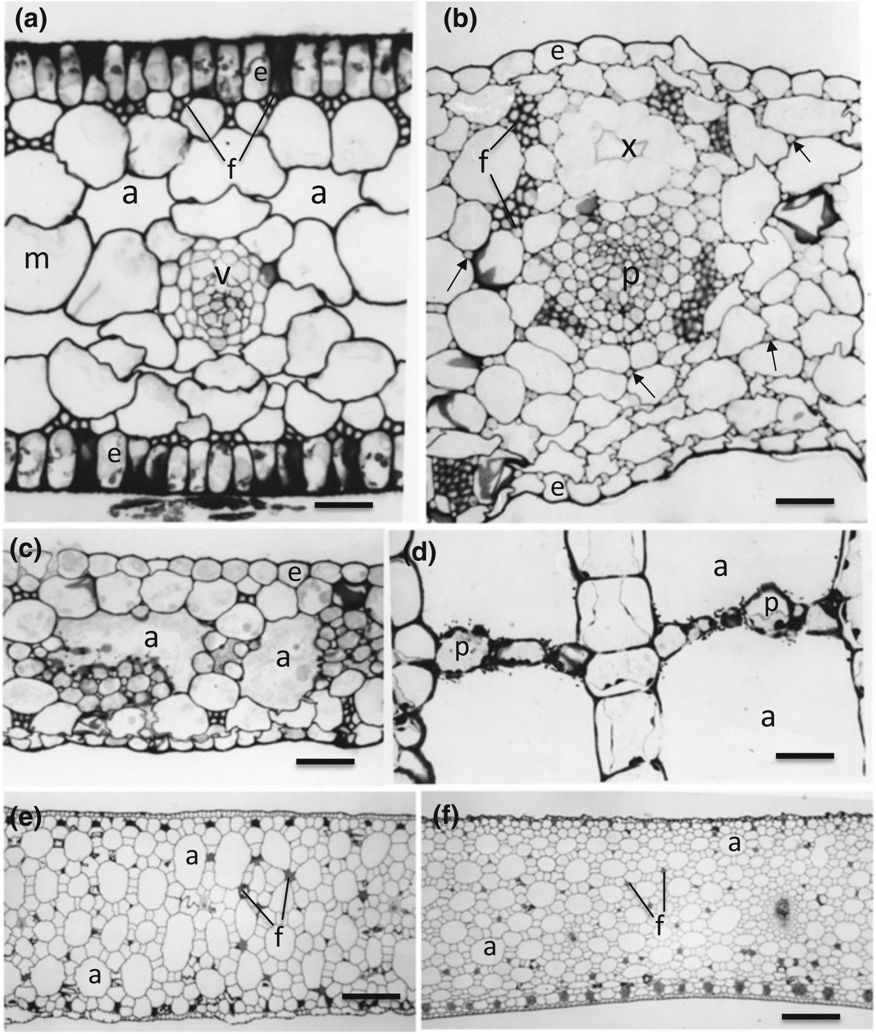


**Fig. 4.4** **a** In *Posidonia australis* leaf blade, fibre bundles (f) mainly associate with epidermal cells (e), irregular sizes of air lacunae (a) present amongst mesophyll tissue (m); both phloem and xylem are enclosed within the vascular bundle (v), scale = 100 µm. **b** Subtidal *Zostera muelleri*, fibre bundles (f) associated with vascular bundles, which have separated phloem tissue (p) and a single lacuna (x). *Note* there are numerous unusual small intercellular fungal hyphae (arrows) among this leaf tissue, scale = 100 µm. **c**, **d** Transverse (**c**) and longitudinal (**d**) sections of air lacunae (a) in *Zostera muelleri* (intertidal), showing a septum consists of a single cell layer of parenchyma cells (p), scales = 50 µm (**c**) and 10 µm (**d**). **e** *Posidonia australis* sheath. **f** *Posidonia coriacea* sheath, scales = 250 µm

thickened walls of the epidermal cells provide tensile strength but retain a high degree of flexibility that allows the strap-like leaf blades to withstand vigorous wave action (Kuo 1978; de los Santos et al. 2016).

## 4.8 Mesophyll and Air Lacunae

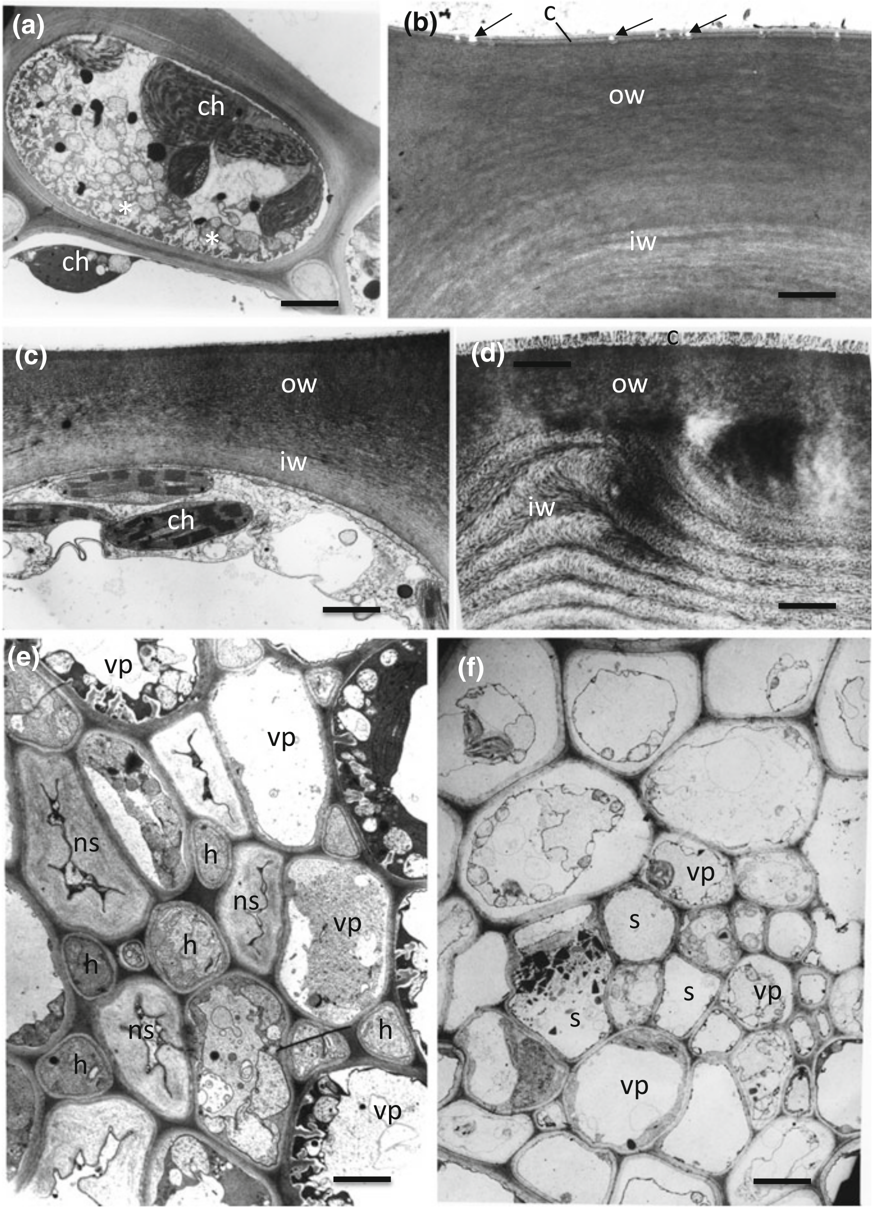
The mesophyll tissue of seagrasses consists of homogeneous, thin-walled but highly vacuolated parenchyma cells. The thin peripheral cytoplasm contains few chloroplasts; some with small starch grains. The mesophyll cells surround air lacunae of varying size; in some genera, e.g. *Cymodocea* (Fig. 4.3b), *Heterozostera*, *Zostera* (Fig. 4.3e), *Syringodium* (Fig. 4.3i) and *Thalassia*, there are prominent and regularly arranged air lacunae separating longitudinal vascular bundles. Air lacunae are less prominent in *Posidonia* (Fig. 4.3j–l) than in the above genera, and they are even smaller in the leaves of *Halophila* (Fig. 4.3c) and *Thalassodendron* (Fig. 4.3h).

There are always regular septa interrupting the air lacunae along the leaf. Each septum consists of a group of small parenchyma cells with minute intercellular spaces (Fig. 4.4c). In the Australian *Zostera*, numerous wall protuberances project into these spaces (Fig. 4.4d). Air lacunae are continuous within all organs (i.e. leaves, petioles, rhizomes and roots) in all seagrass species. These septa provide a physical barrier to flooding but allow gas continuity to be maintained within the lacunal system (Roberts et al. 1984).

## 4.9 Leaf Vascular System

The strap-like leaves of seagrasses have several parallel longitudinal vascular bundles, which are connected by smaller transverse bundles. The ovoid leaves of *Halophila* also have pinnate venation, with cross veins connecting the mid rib and the marginal vein. Vascular systems in seagrasses are similar in structure and composition to those in vascular land plants, and all have sieve elements, xylem elements and vascular parenchyma cells. Distinct sheath cells enclose each longitudinal vascular bundle of the leaf. The wall of the bundle sheath cells differs between genera; it is thin and lignified in *Posidonia* (Kuo 1978) or suberized in *Syringodium* (Kuo 1993a); thick and suberized in *Thalassodendron* and *Amphibolis* (Kuo 1983a; Barnabas and Kasavan 1983); with wall ingrowths in the inner tangential walls in *Zostera* and *Heterozostera* (Kuo 1983a); or without obvious structural specialization in *Enhalus*, *Thalassia* and *Halophila*. Kuo (1993a) speculated that solute transfer might be restricted to a symplastic pathway between the mesophyll and vascular tissue in the species that have suberisation or lignification in sheath cells.

Sieve elements in seagrasses are of two main types: nacreous-walled elements (Fig. 4.5e) in *Zostera*, *Heterozostera*, *Halodule* and *Halophila*, but all other seagrasses have normal thin-walled sieve elements (Fig. 4.5f). In addition to normal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◀**Fig. 4.5** Ultrastructure of seagrass leaf blades. **a** *Zostera muelleri* leaf blade epidermal cell contains many chloroplasts (ch) and other organelles. *Note* wall-ingrowths (*) are present on the inner tangential walls, scale = 2 µm. **b** The outer tangential wall of *Z. muelleri* epidermal cell has two distinct zones: an outer electron-compact layer (ow) and an inner loose layer (iw). A thin cuticle (c) has several small invaginations (arrows), scale = 1 µm. **c** *Syringodium isoetifolium* has a very thin cuticle and two distinct wall zones (ow, iw), scale = 1 µm. **d** *Amphibolis antarctica* has a porous cuticle and two distinct wall zones, the inner one (iw) has a wavy appearance, scale = 1 µm. **e** Subtidal *Zostera muelleri* vascular tissue. Unusual living fungal hyphae (h) are closely associated with nacreous sieve tubes (ns) and vascular parenchyma cells (vp), scale = 5 µm. **f** *Syringodium isoetifolium* vascular tissue has normal thin walled sieve tubes (s) and vascular parenchyma cells (vp), scale = 4 µm

thin-walled sieve tubes, there are also a few small thick walled sieve tubes with smooth inner surfaces and reduced lumens. These unusual sieve tubes only occur near xylem elements in *Thalassodendron* (Barnabas 1983) and *Syringodium* (Kuo 1993a). The unlignified nacreous wall has an uneven inner surface due to irregular wall thickening. The increased wall thickness in nacreous-walled sieve elements is usually accompanied by a reduction in cell lumen, not an increase in the size of an element. Both normal and nacreous-walled sieve elements have similar cytoplasmic properties (Kuo 1983b). Whether the uneven lumen size along the nacreous sieve tube length could be significant to translocation remains to be determined.

The number and size of xylem elements in the vascular bundles of seagrasses, as in other aquatic plants, are much reduced in comparison with those in vascular land plants. The xylem in *Heterozostera* and *Zostera* is represented by a wide lacuna surrounded by a distinct layer of large xylem parenchyma cells with thickened but not lignified walls (Fig. 4.4b). Ultrastructurally, the original xylem wall appears to be completely hydrolyzed and the ‘xylem wall’ is represented only by the middle lamella together with the thickened wall of the xylem parenchyma cells abutting the xylem element (Kuo et al. 1990). In other seagrasses the xylem may consist of several elements with highly hydrolyzed walls and little (e.g. *Posidonia*) or no lignification (other genera). The structure of phloem and xylem parenchyma cells is very similar in all seagrasses, except for the Zosteraceae, in which wall ingrowths occur in phloem parenchyma cells. Barnabas (1988, 1989, 1994) used an apoplastic tracer to demonstrate water movement in the leaves of *Thalassodendron ciliatum and Halodule uninervis.*

## 4.10 Leaf Sheath

Leaf sheaths are present in all seagrass genera, except in *Halophila*. Leaf sheaths are clearly differentiated from leaf blades, and enclose the young, developing leaves. The leaf sheaths are usually covered by sediment, at least at the base. At the junction of sheath and blade a structure known as a ligule is produced as an adaxial outgrowth.

The general anatomy of the leaf sheath is similar to that of the leaf blade (see above), but there are differences in detail. The vascular bundles are similar to those in the blade but there are no cell wall ingrowths in the vascular sheath and phloem parenchyma (Zostera, Heterozostera). Fibre bundles and air lacunae are more pronounced in the sheath than in the blade (Fig. 4.4e, f). Furthermore, in contrast to those in the blade, the fibre bundles of the sheath are lignified, and then persist on the rhizomes long after the other tissues of the leaf sheath have rotted away, for example in *Posidonia* (Kuo 1978). The sheath fibres of *Posidonia* are rolled by wave action to form ‘marine balls’ of different sizes. The epidermis of the sheath lacks chloroplasts and cell wall ingrowths, has a non-porous cuticle (*Posidonia*), or lacks subcuticular cavities (*Zostera*) and so it probably has no function in the performance of photosynthesis. The leaf sheath appears to have an important role in cell expansion of the growing leaf: in *Posidonia*, a standing osmotic gradient is maintained against external salinity for the fluid surrounding the expanding leaf emerging from the basal meristem (Tyerman et al. 1984; Tyerman 1989).

## 4.11 Stems (Erect Shoots) and Rhizomes

Seagrass rhizomes are usually herbaceous, cylindrical to laterally compressed, and monopodially or irregularly branched. The rhizomes of *Halophila spinulosa* are however hard, and those of *Amphibolis* and *Thalassodendron* become woody. Rhizomes are almost always buried under sediment, and are usually covered with the persistent, fibrous remains of old leaf sheaths, for example in *Posidonia* and *Enhalus*. Some seagrasses (*Thalassia*, *Halophila spinulosa*, *H. tricostata*, all Cymodoceaceae, and *Heterozostera nigricaulis*) have a dimorphism of vegetative axes, at certain nodes they give rise to erect stems bearing leafy shoots. Tomlinson (1974) emphasised the importance of rhizome growth in the extension of seagrass meadows, and more recent work has reviewed the role of seed production in dispersal of species (Kendrick et al. 2012). Unusual forms of vegetative propagation have been described in an Australian Zosteraceae species (Cambridge et al. 1983) and in *Amphibolis* (Kuo et al. 1987). These forms may represent further means of reproductive propagation, with consequences discussed in Sinclair et al. (2016a, b).

The internodes of rhizomes and erect shoots (if present) appear similar in transverse section. The outermost layer is an epidermis covered by a distinct cuticle, and may contain tannin. The bulk of rhizome and stem is cortical tissue, the structure of which may vary with different genera. There may be a distinct hypodermis, the outer most layer of cortical tissue, with a thickened wall and suberized middle lamella (e.g. *Posidonia*, *Halophila*). In this cortical tissue large lacunae may develop, as in *Enhalus*, *Syringodium*, and *Halophila*, and may contain cortical vascular and/or fibre bundles; the distribution and number of which appears to be constant within each genera. Starch accumulates in the cortical parenchyma cells in some genera (*Enhalus*, *Thalassia*, *Halodule*), but not in *Amphibolis* or *Thalassodendron*. These two genera have two distinct regions in the rhizome cortical tissues; the outer cortical parenchyma having thick, lignified walls and the inner one having thin, non-lignified walls (Fig. 4.6h–j). The innermost layer of cortical cells in all genera is the endodermis, which surrounds the central stele

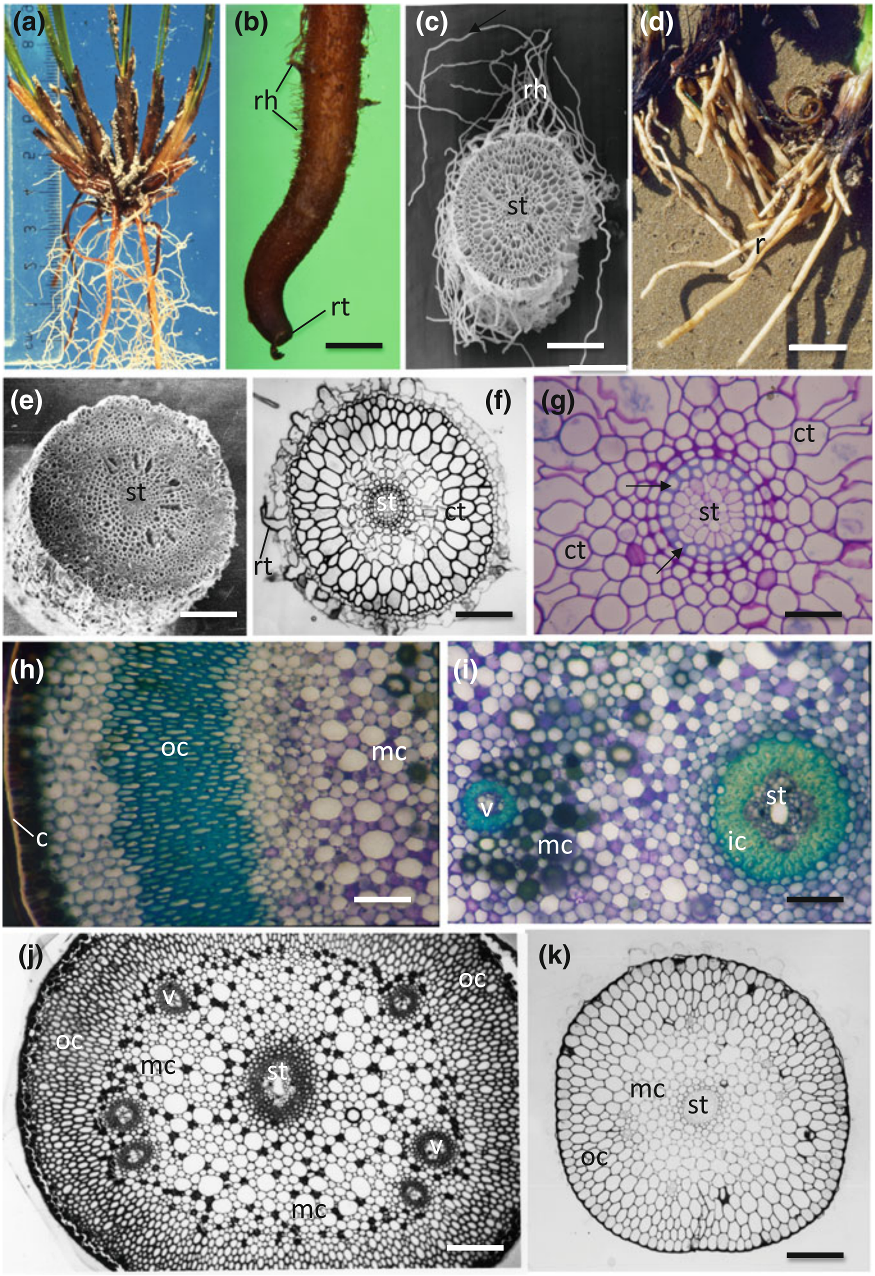
(Fig. 4.6i, j). The endodermis may either become suberized (e.g. *Posidonia*, *Halodule*) or have thickened and lignified walls (*Amphibolis* and *Thalassodendron*) surrounding the central stele (Fig. 4.6i, j). A central stele contains one or more larger central protoxylem elements surrounded by sieve tubes; the pericycle is not distinct.

## 4.12 Root

The roots of seagrasses are adventitious as in all monocotyledons, and arise from the ventral side of the rhizome nodes. Although the internal anatomy is generally similar, the external morphology of roots often has characteristic features in different taxa, with many specialized features thought to be adaptations to different substrates in an aquatic environment.

The external morphology of roots often has characteristic features in different taxa, with adaptation to different substrates, though the internal anatomy is generally similar. Roots of *Zostera* and *Heterozostera* always occur in two groups, each of which bears 2–12 unbranched roots with numerous long root hairs (Fig. 4.6c). Roots of *Posidonia* are thick, soft and extensively branched, but root hairs are rare (Fig. 4.6e). *Syringodium*, *Cymodocea* (Fig. 4.6f) and *Halodule* have, at each rhizome node, one or more moderately branched roots with few root hairs. The roots of *Amphibolis* are wire-like, moderately branched, with no root hairs (Fig. 4.1a). *Thalassodendron pachyrhizum* roots are thick and extremely strong with a shiny black surface, and rarely branched. Its short root hairs are concentrated in a small zone near the root tip (Fig. 4.6b), whereas *T. ciliatum* produces wiry, moderately branched roots. *Enhalus* usually grows in muddy sand substrates and bears several coarse, soft, unbranched roots with few short root hairs (Fig. 4.6d). *Thalassia* and most of the *Halophlia* species (Fig. 4.1a, f) produce a single unbranched root with numerous long root hairs, particularly when growing in sandy calcareous sands, while *H. spinulosa* possesses a hard, wiry root with fewer root hairs. Among the seagrasses, unbranched roots seem characteristic of certain genera, and their occurrence appears strongly correlated with the presence of root hairs; so that the total root surface area may well be similar in seagrasses with either unbranched or branched roots.

Anatomy and histochemistry of root tissues may vary with different species reflecting their external morphology. Roots of all seagrasses have a distinct root cap protecting the root meristems. The mature root has an epidermis, which may bear root hairs, overlaying cortical parenchymatous tissue that encloses air lacunae and a central stele (Fig. 4.6c, e–g). The epidermal cells usually have thin, unlignified walls and a peripheral cytoplasm, and below the epidermis there is a distinct exodermis one or more cells thick, each of which has thickened but unlignified walls containing suberin lamellae. The root epidermis of *Posidonia* is lignified but the exodermis is not, and in hard roots, such as those of *Thalassodendron* and *Amphibolis*, the walls of the epidermal cells and three or more layers of exodermal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◀**Fig. 4.6** Roots and rhizomes in seagrasses. **a** *Posidonia sinuosa*. **b** A root-tip of *Thalassodendron pachyrhizum*, scale = 1 mm. **c** Cross section of a *Syringodium* root, scale = 1 mm. **d** Whitish cord roots of *Enhalus acoroides*, scale = 3 mm. **e** Cross section of a *Posidonia australis* root, scale = 2 mm. **f** Cross section of *Halodule uninervis* roots, scale = 200 µm. **g** Cross section of a *Syringodium* root, scale = 50 µm. **h** Peripheral portion of *Thalassodendron pachyrhizum* rhizome. **i** Central portion of *T. pachyrhizum* rhizome, scales = 100 µm. **j** Cross section of *Amphibolis griffithii* rhizome, scale = 500 µm. **k** Cross section of *Halophila spinulosa* rhizome, scale = 200 µm, c: cuticle, ct: cortex, ic: inner cortex, mc: middle cortex, oc: outer cortex, r: roots, rh: root hairs, rt: root tip, st: stele, v: cortical vascular bundles, arrows in (**g**): the endodermis with lignified walls

cells are thickened and lignified (Kuo 1983a; Barnabas 1996). The cortex usually has three distinct zones: (a) An outer layer with larger cells; (b) the middle cortex with a system of large air lacunae separated by radial partitions one cell thick containing small intercellular pores; and (c) an inner cortex consisting of compact, small cells in a regular, concentric arrangement (Fig. 4.6c, e, f).

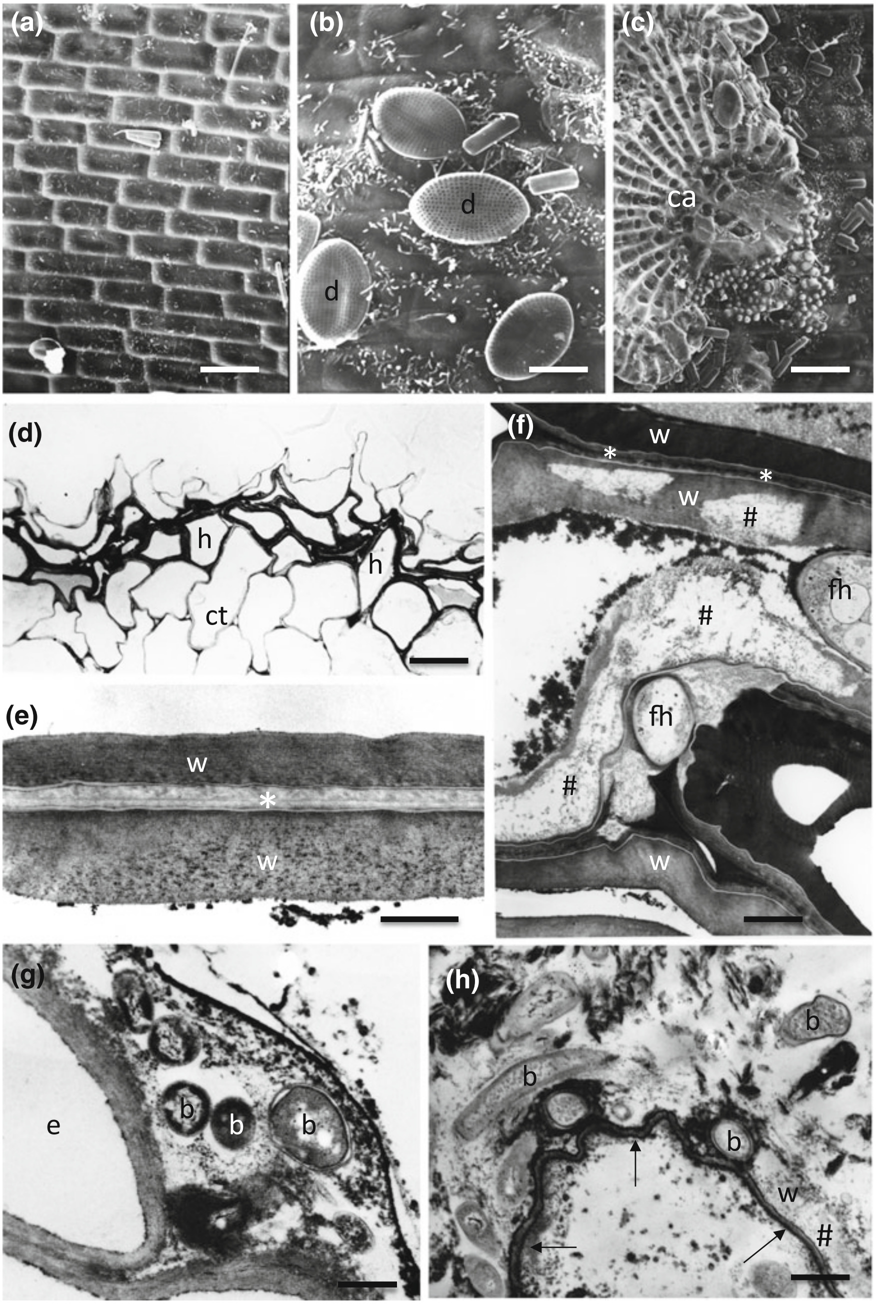
As in their terrestrial monocotyledon cousins, the stele of seagrass is surrounded by a layer of small, compact endodermal cells with thin to moderately thick walls, either lignified (suberized) (Fig. 4.6g) or non-lignified. A distinct Casparian strip is always present in the radial walls of endodermal cells. The stele contains several normal walled sieve tubes and a few, poorly-lignified or not lignified tracheid elements (e.g., *Posidonia*, *Zostera*). There are a few vascular parenchyma cells but no distinct pericycle tissue. However, vascular parenchyma cells within the stele of *Zostera* have transfer cell features. The suberin lamella in the exodermis and the Casparian strip in the endodermis presumably restrict exchange of solutes and water, as they do in many terrestrial plants (Kuo and Cambridge 1978).

Roberts et al. (1985) found that sieve tube are differentiated before xylem elements in the developing root of *Halophila ovalis* and that the occurrence of root hairs, the Casparian strip formation and xylem differentiation were approximately synchronous, suggesting that all structures are involved in the uptake and transport of materials. Root hair structure and development in *H. ovalis* has been described by Roberts (1993).

## 4.13 Phyllosphere, Rhizosphere and Endophytes

The leaves and erect stems of seagrasses often bear various epiphytes including bacteria, diatoms, algae, hydroids and sponges. The attachment of epiphytes to the seagrass host appears to be restricted to the cuticle of the host epidermis (Fig. 4.7a–c) and these epiphytes have not been observed to penetrate into the host epidermis and beyond.

Supaphon et al. (2014) and García et al. (2005) showed that roots of the Mediterranean *Posidonia oceanica* had a higher microbial abundance than those of the Australian *P. australis* and *P. sinuosa.* Microbial density tended to decrease as root order increased, and living roots always showed higher microbial abundance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◂**Fig. 4.7** Epiphytes and rhizosphere. **a–c** SEM images showing various epiphytes occur on the leaf blade surface of *Posidonia ostenfeldii* in the earlier stage only a few bacteria (**a**), then more bacteria and diatoms (d) (**b**); then bacteria, diatoms and calcareous red algae (ca), scale bar = 20 µm. **d–h** Rhizosphere: **d**, **e** *Posidonia* roots have one to two layers of thick walled hyperdermis (h) in the outermost cortex (ct), scale bar = 30 µm. **e** These thickened walls (w) have a suberin lamellae (asterick) present on the walls (w) of two adjacent hyperdermal cells, scale bar = 1 µm. **f** Fungal hyphae (fh) are lysing the thickened wall (w) materials that appeared as electron transparent fibrous material (#), scale bar = 2 µm. **g** Bacteria colonies (b) often observed on the surface of root epidermal cells (e), scale bar = 1 µm. **h** Bacterial colonies (b) are lysing thickened wall material and leaving suberin lamellae (arrows) intact, scale bar = 1 µm

than dead ones. These authors suggested that root age influences the rate of microbial colonization of seagrass roots and that colonization of root surface by microorganisms is associated with organic exudates from the roots rather than with decaying root tissues.

The rhizosphere of many seagrasses has been found to support a diversity of microorganisms, especially bacteria. These occur mainly on the root surface, with tissue penetration rarely occurring, and then only into the periphery of the host (Kuo 1983a). Some of these organisms may penetrate the epidermal cells and lyse the thick polysaccharide materials of both epidermal and exodermal cells. These organisms are absent from the meristem regions, deep cortical tissues and the stele, as well as from the root cap rhizosphere (Kuo 1993b). Fungi were found to have penetrated the epidermal cells of *Posidonia* causing lysis of the thick polysaccharide material in the walls of the exodermal cells. A suberin lamella restricts penetration, but fungi and bacteria occur in the lumen of exodermal and outer cortical cells (Kuo et al. 1981). In addition, bacteria colonies are found on the outer surface of epidermal cells, embedded among substratum materials in tropical species, *Thalassia*, *Cymodocea*, *Syringodium* and *Halodule*. As with terrestrial plants, it has been suggested that rhizosphere microorganisms may be involved in nutrient uptake and nitrogen fixation in seagrasses (Kuo et al. 1981).

Recently, there have been several reports of "endophytes" from tropical and temperate seagrasses (Küsel et al. 1999; Devarajan et al. 2002; Sakayaroj et al. 2010; Garcias-Bonet et al. 2012; Torta et al. 2015; Venkatachalam et al. 2015). It seems that these bacterial and fungal assemblages were isolated from freshly collected, cleaned and sterilized vegetative segments and then cultured. As these studies were not accompanied by with the images of their studied tissues, it is not certain whether these endophytic assembles were present in the internal living tissues as true endophytes. Vohnik et al. (2015) presented excellent micrographs showing an endophytic fungus present in the *Posidonia oceanica* root tissues, but it was dead and not the living tissues. Unusual apoplastic fungal hyphae were however observed throughout the living leaf intercellular spaces of the subtidal *Zostera muelleri* from Swan Bay, Victoria (Kuo 1984; Kuo et al. 1990; *see* also Figs. 4.4b, 4.5e). Hyphae were branched in mesophyll tissues but they avoided the leaf surface, the septa in the air lacunae system and some xylem elements. The hyphae were completely embedded in the intercellular substance and cell walls of host tissues, but did not enter the cytoplasm of the host cells. These fungal hyphae were not found in the roots and rhizomes of the same plant nor from all vegetative organs of the intertidal *Z. muelleri* from the same locality. It has been speculated that these apoplastic fungi might be involved in enhancing solute transfer within the seagrass leaves (Kuo 1984).

## 4.14 Reproduction: Flowers, Fruits, Seeds and Seedlings (See also Table 4.3)

Seagrasses are unique in their capacity for a hydrophilous pollination, and producing seeds in high salinity environments in order to complete their life cycle. Many species also form fruits to carry the seeds.

Seagrass plants have two flowering forms: in the first, either male and female flowers are born on the same plant (monoecious) as in the Posidoniaceae (Fig. 4.7a, b), Zosteraceae (Fig. 4.7c, d), *Halophila decipiens* (Fig. 4.7f) and *H. capricorni*. In the second, the male and female flowers occur on separate plants (dioecious), as present in the entire Cymodoceaceae (Fig. 4.7h, i), *Enhalus* (Fig. 4.1d), *Thalassia* (Fig. 4.7m) and most of the *Halophila* species (Fig. 4.7k, l).

The ultrastructure of pollen, pollen development and stigma surface in *Thalassodendron*, *Amphibolis* and *Posidonia* and *Thalassia* were described by Ducker et al. (1978), McConchie et al. (1982a, b), McConchie and Knox (1989a, b) and Pettitt (1976, 1980, 1984).

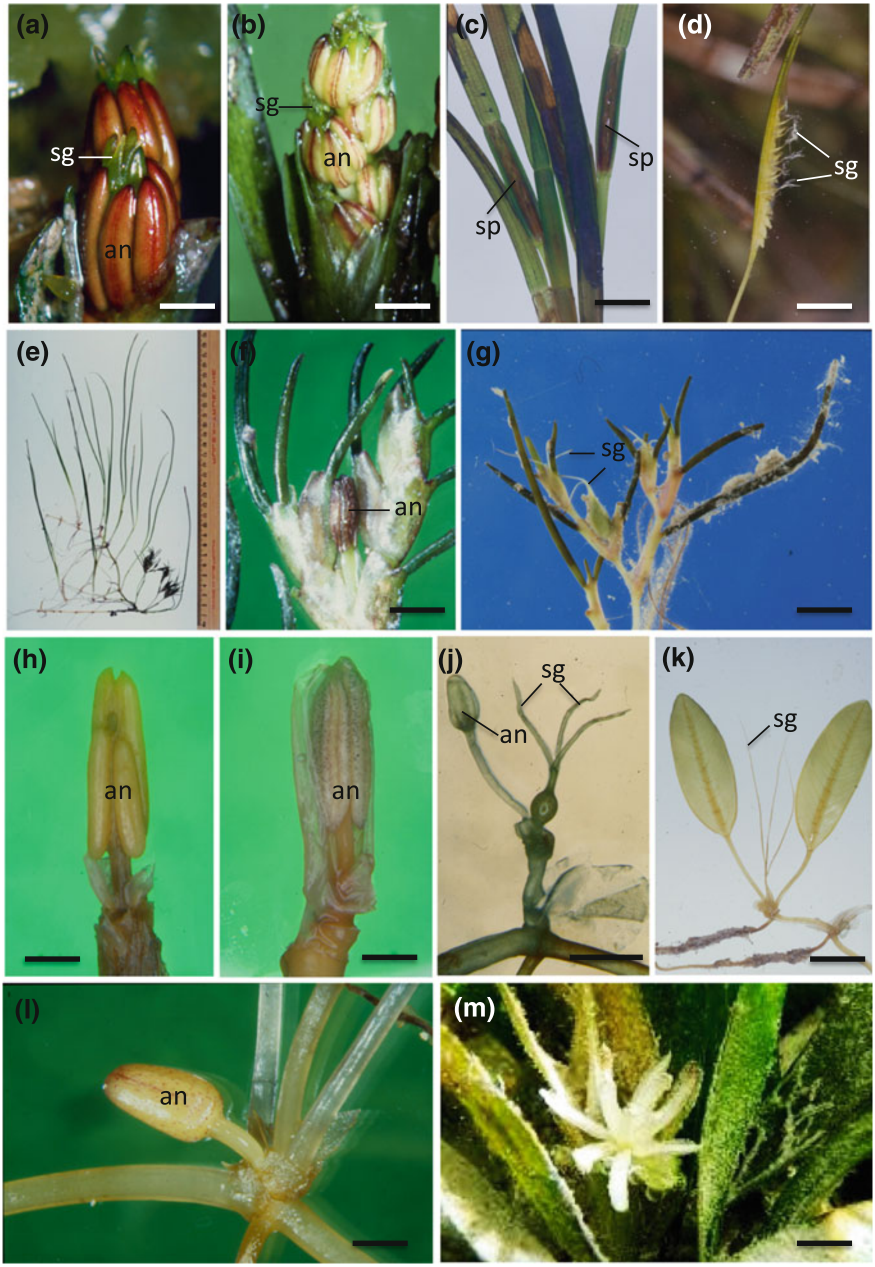
The Zosteraceae (*Zostera* and *Heterozostera*) have a unique flower morphology among the angiosperms with the inflorescences (spadices), consisting of flowers on flattened, spike-like axes, with two stamens and one pistil arranged alternately in two longitudinal rows. Each axis is enclosed by a modified leaf sheath (spathe) (Fig. 4.7c), and bears structures termed retinacula at regular intervals along the margin. The stamen has two bi-locular anthers, and the pistil bears a single carpel with two slender stigmas. During pollination, anthers slit longitudinally to release filamentous pollen grains that twist around the stigma. After fertilization, the carpel grows, matures and formes an achene fruit with a scarious pericarp and a hard, fibrous endocarp.

*Posidonia* has racemose inflorescences with leafy bracts; the ultimate unites are spike-like, with several apparently naked flowers on long peduncles. The flowers are bisexual, each with three stamens, a single carpel containing one ovary and no perianth parts (Fig. 4.8a, b). The mature stamens slit longitudinally and release thread-like pollen grains containing vegetative and sperm nuclei for attachment to the stigma surface. Ma et al. (2012) and Remizowa et al. (2012) contributed detailed studies of the megasporogensis and embryogenesis in the Australian *Posidonia.* Ma et al. (2012) reported that the mature embryo sac is of Oenothera-type (monosporic, 4-celled, unipolar) and is comprised of one central cell containing polar nucleus, one egg cell and two syngerids. After fertilization, the fertilized egg divides longitudinally into two. The basal cell ceases division and may function as a conduit for nutrients to the upper, dividing cell(s). The upper cell firstly divides transversely into

**Table 4.3** Reproductive features of Australian seagrasses

| Genera | Flowers | Pollen | Fruits | No. seeds per fruit | Main nutrient storage in seeds | Seeds covering | Dormancy |
|---|---|---|---|---|---|---|---|
| *Enhalus* | Dioecious | Grains | Soft | Several | Starch | Membranous | Not distinct |
| *Thalassia* | Dioecious | Grain in chain | Soft | Several | Starch | Membranous | Not distinct |
| *Halophila* | Monoe/ dioecious | Grains in chain | Soft | Several | Starch | Hard | Distinct |
| *Posidonia* | Monoecious | Filiform | Soft | One | Starch | Membranous | Not distinct |
| *Cymodocea* | Dioecious | Filiform | Hard | One | Starch | Hard | Distinct |
| *Halodule* | Dioecious | Filiform | Hard | One | Starch | Hard | Distinct |
| *Syringodium* | Dioecious | Filiform | Hard | One | Starch | Hard | Distinct |
| *Amphibolis* | Dioecious | Filiform | Viviparous | One | [a] | – | – |
| *Thalassodendron* | Dioecious | Filiform | Viviparous | One | [a] | – | – |
| *Zostera* | Monoecious | Filiform | Hard | One | Starch | Hard | Distinct |
| *Heterozostera* | Monoecious | Filiform | Hard | One | Starch | Hard | Distinct |

[a] The embryo of *Amphibolis* and *Thalassodendron* does not accumulate starch but obtains the nutrients required directly from the parent plants through specialised transfer cells at the interface of developing seed and the parent tissue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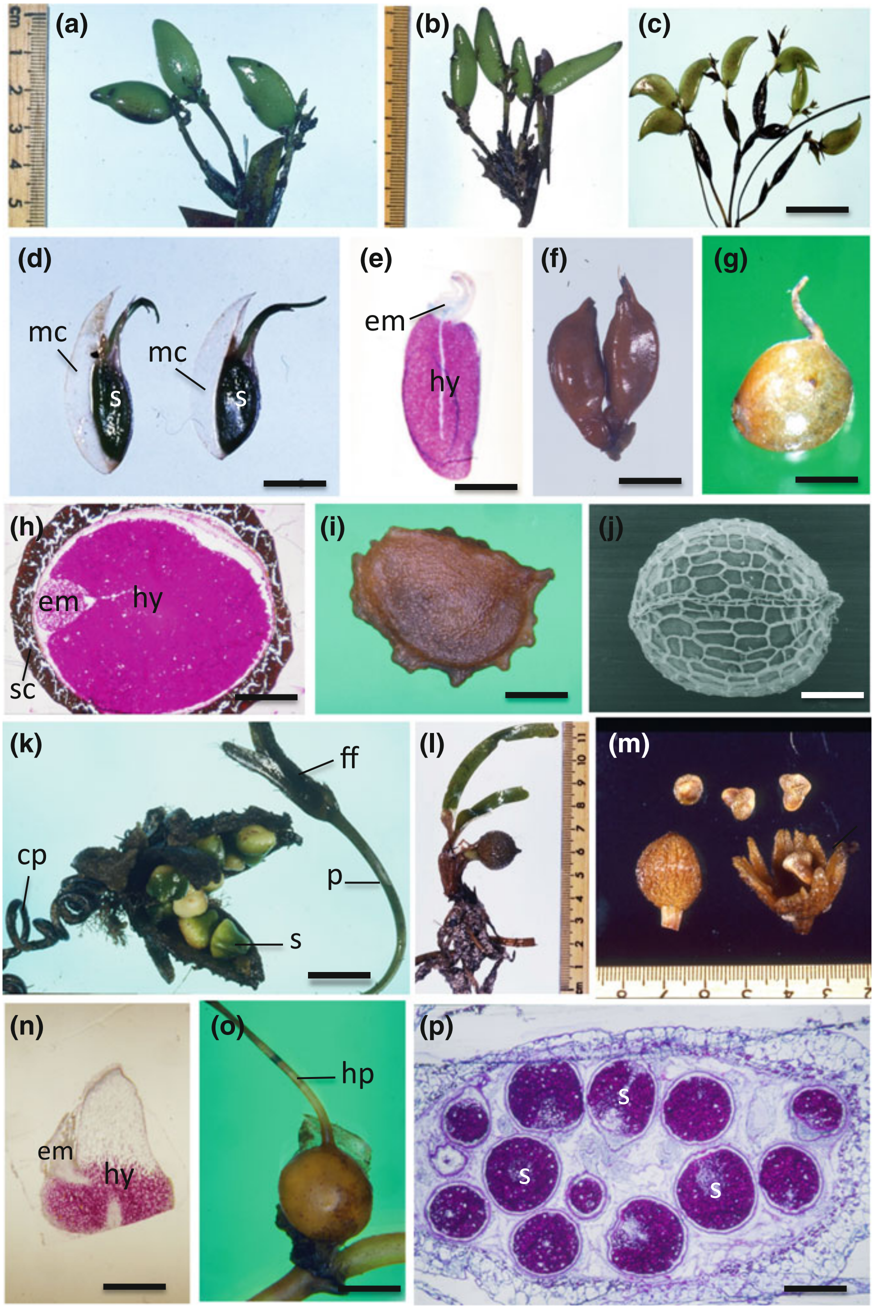
◀**Fig. 4.8** Flowers in seagrasses. Monoecious flower of *Posidonia australis* (**a**) and *P. sinuosa* (**b**) has a disc-like stigma (sg) and three anthers (an), scale = 5 mm. **c** Monoecious flowers of *Zostera capricorni* are formed on the spathes (sp), scale = 8 mm. **d** Stigmata (sg) of *Z. capricorni* flower, scale = 6 mm. **e–g** Flowers of *Syringodium isoetifolium*, **f** Male flower with anthers (an), **g** Female flowers with two stigmata (sg), scale = 5 mm. **h** *Halodule uninervis* male flower has two unequal height of anthers (an), scale = 1.5 mm. **i** *Cymodocea serrulata* male flower has two equal-height anthers (an), scale = 1.5 mm. **j** Monoecious flowers of *Halophila decipiens* have both male (an) and female (sg) flowers formed on the same floral shoot, scale = 4 mm. **k** *Halophila ovalis* female flower has three elongated stigmata (sg), scale = 1 mm. **l** *H. ovalis* male flower has a colourful anther (an), scale = 3 mm. **m** *Thalassia hemprichii* male flower (*credit* Dr. F. Short)

two cells and then longitudinally into four cells that in turn develop into a globular zygotic embryo attached by the basal cell (suspensor). The globular zygotic embryo morphs into a shuttle-shaped embryo and loses attachment to the basal cell (Ma et al. 2012; Remizowa et al. 2012). The fruits mature about three months after fertilization (Fig. 4.9a–c). The fruits are soft when shed in November to January, have a fleshy pericarp, and are positively buoyant. The plants are not viviparous, but the seeds show little or no dormancy phase. The embryo has an enlarged hypocotyl, a short radicle and is covered by a thin membrane (Fig. 4.9d). After a day or two, each fruit splits longitudinally and releases a seed, which already germinated and is negatively buoyant. The hypocotyl contains mainly starch (Fig. 4.9e) and may remain attached to the seedling for up to eighteen months but most of the food reserves are used within the first 5–7 months (Hocking et al. 1981; Statton et al. 2014). The accumulation of nutrient reserves in seeds and their utilization during germination and seedling establishment have been described for two Australian *Posidonia* species (Hocking et al. 1980, 1981), with nitrogen, phosphorus and other macro and microelements present in concentrations comparable to those in terrestrial plants.

In the Cymodoceaceae, the flowers are usually solitary, and terminal on erect shoots (*Halodule*, *Cymodocea*) or their branches (*Amphibolis*, *Thalassodendron*), but are arranged as distinct cymose inflorescences in *Syringodium* (Fig. 4.8e–g). The vascularization of the reproductive system is similar in all members of the family, and has been described for *Amphibolis* (McConchie et al. 1982a). Both male and female inflorescences are surrounded by several alternate sheath-like bracts. Each male flower is either subsessile or stalked and has two anthers, which are laterally fused and bear two or three apical appendages on each lobe. Each inflorescence in the family consists of two morphologically identical flowers, which develop in the same way, except for the male flower in *Thalassodendron*, which has two morphologically identical but developmentally different flowers (Fig. 4.8i) to prolong the pollen production period and so increase the chance of fertilization (Kuo and Kirkman 1987). It has been estimated that an inflorescence in *T. pachyrhizum* is produced three or more years after an upright stem has emerged, and that no more than 10% of stems in the field bear inflorescences in a particular year (Kuo and Kirkman 1987). It is still not clear if one flowering stem will produce inflorescences for more than one season. In *Halodule*, the anthers are unequal in height (Fig. 4.8h) and the female flower is sessile or with a short pedicel, and has two free carpels; each with either a simple style (*Halodule*) or a style with two to three slender stigma (other genera).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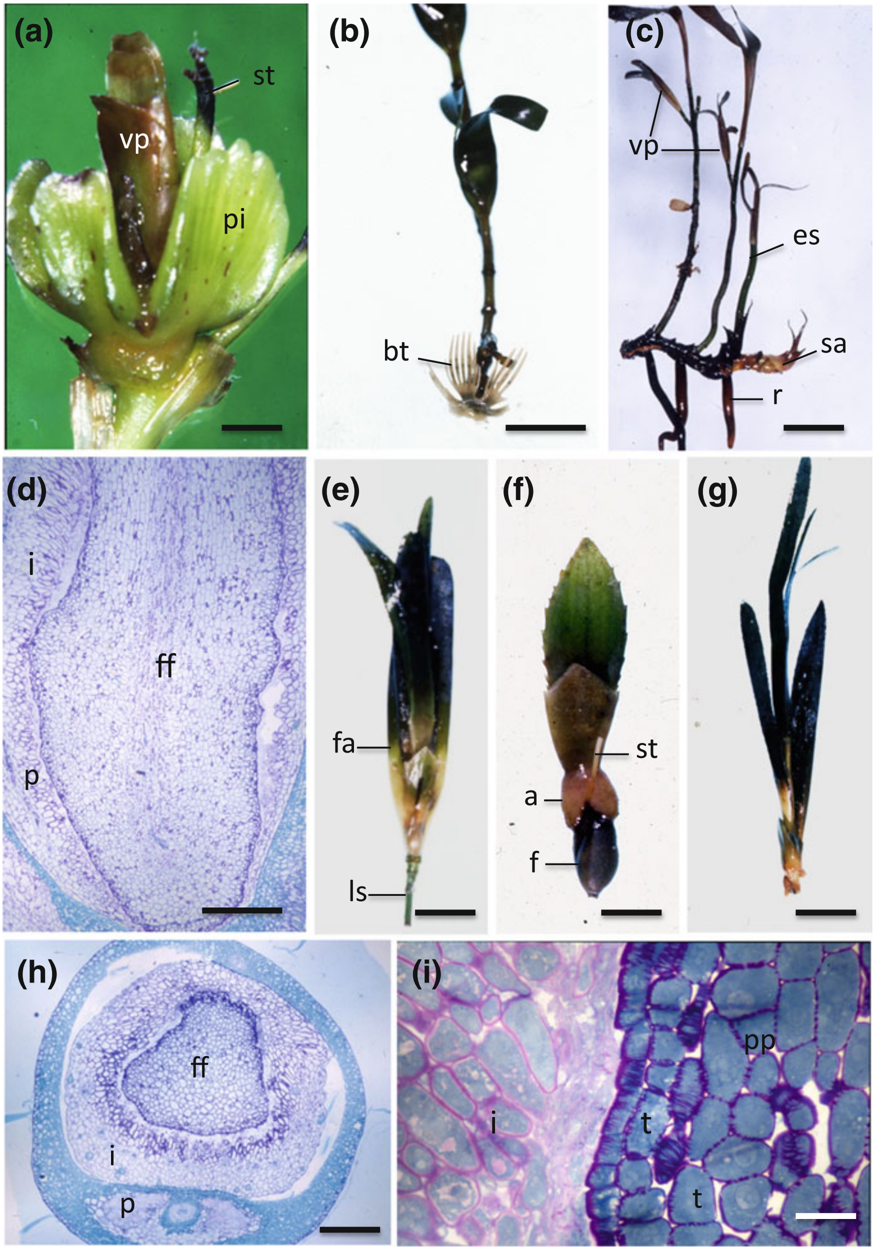
◂**Fig. 4.9** Fruits and seeds in seagrass. **a** *P. australis* fruits. **b** *P. sinuosa* fruits. **c** *P. denhartogii* fruits, scale = 1.2 cm. **d** *P. coriacea* seeds, with membranous seed coats (mc). **e** *P. australis* seed has a large starch storage hypocotyle (hy) and a distal plumule (em), scale = 1 mm. **f** Fruit/seed of *Cymodocea rotundata*, scale = 1 mm. **g** Fruit/seed of *Halodule uninervis*, scale = 1 mm. **h** *H. uninervis* seed has a thick seed coat (sc) and a large starch storage hypocotyle (hy) and a small plumule (em), scale = 4 mm. **i** Fruit/seed of *Cymodocea serrulata*, scale = 2 mm. **j** *Halophila australis* seed coat surface has a regular pattern, scale = 200 µm. **k** *Enhalus acoroides* fruit supported by a coiled peduncle (cp) forms several triangular seeds (s). *Note* young female flower (ff) has a straight peduncle (p), scale = 1 cm. **l** *Thalassia hemprichii* fruit attaching to the plant. **m** A mature fruit of *T. hemprichii* fruit releasing several angular seeds **n** *T. hemprichii* seed has a large starch storage hypocotyle and an emerging plumule (em), scale = 2 mm. **o** *Halophila ovalis* fruit has an elongated sterile part of the ovary (hp), scale = 3 mm. **p** *Halophila tricostata* fruit contains several starch-rich seeds (s), scale = 500 µm

*Cymodocea*, *Halodule* (Kuo and Kirkman 1990) and *Syringodium* in the Cymodoceaceae produce indehiscent fruit with stony pericarps (Fig. 4.9f–i), but in *Syringodium*, only a stony endocarp is retained with a fleshy exocarp being lost during fruit development (McMillan and Bragg 1987). The embryo of these seagrasses has a reduced radicle adpressed to an engaged structure that is interpreted either as an expansion of the radicle itself or as an adnate hypocotyl, which stores mainly starch (Fig. 4.9h). The cotyledon and plumule are folded into a hypocolary invagination along the line of wall separation. A radicle hump or short radicle develops during germination (Bragg and McMillan 1986). In the tropical species *C. rotundata*, germination can occur throughout the years. Longevity of seeds varies from seeds that may be dormant for long periods, possibly for many years such as *Halodule*, or of *Syringodium*, which are able to germinate for more than three years after seeds have been released from the parent plant; the longevity of seeds of these species may well exceed that of other seagrasses. In contrast, seeds of *Posidonia* have no dormancy (Ostenfeld 1916; Kuo and Kirkman 1996; Statton et al. 2013).

*Amphibolis* and *Thalassodendron* produce viviparous seedlings (Fig. 4.10c). The embryo of *Amphibolis* has a long cotyledon, a short axis and no radicle, and it develops a leafy shoot, which remains attached to the parent for about 6–8 months. There are four fleshy, herbaceous pericarp lobes at the base of the ovary (Fig. 4.10a), these become hard and have fine bristles united at the base, and form a 4-lobed ‘comb’, or ‘grappling apparatus’ (Black 1913; McConchie et al. 1982a, *see* also Fig. 4.10b). This appears from the ovary wall late in the development of the flower, although its initials are present prior to fertilization (McConchie et al. 1982a). Tepper (1882) regarded the grappling apparatus as tepals while Tomlinson and Posluszny (1978) refer to them as sepals. An abscission layer forms immediately below the comb, releasing the seedling. The grappling apparatus becomes caught in a substratum such as algal turf on reefs or fibres from leaf sheaths of *Posidonia*, subsequently roots develop and the grappling apparatus remains on the plant for another 6–12 months.

In *Thalassodendron*, the innermost bracts continue to develop after fertilization, and eventually enclose the carpels to form a false fruit (Fig. 4.10d). Normally only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◂**Fig. 4.10** Viviparous reproduction in seagrasses. **a** A young viviparous seeding (vp) supported by an enlarging pericarp (pi) on the parent plant of *Amphibolis antarctica*, st, stigma, scale = 500 µm. **b** *A. griffithii* seedling with bristles (b) of the grappling apparatus, scale = 500 µm. **c** Viviparous seedlings (vp) form on *Thalassodendron pachyrhizum* erect stems (es). Note the plant has thick, dark roots (r) and a shoot apex (sa), scale = 1 mm. **d** A developing viviparous seedling of *T. pachyrhizum* is protected by a false fruit (fa) and still attached to the parent's stem (ls), scale = 500 mm. **e** A close up view of a developing viviparous seeding, a: aril-like structure; f: fruit; st: stigma, scale = 250 mm. **f** A mature seedling detached from the parent plant, scale = 500 µm. **g–i** Anatomy of viviparous seedlings of *T. pachyrhizum*. longitudinal (**g**) and transverse (**h**) sections and **t**he interface of seedling and the parent tissue (**i**) showing numerous protein rich transfer cells (t) and lacking starch, ff: growing viviparous seedling; i: interface; p: parental tissue; pp: seedling parenchyma cells, scales = 50 µm

one carpel is fertile, and a seed from this carpel germinates on the parent plant probably in April to June (Isaacs 1969; Kay 1971; Kuo and Kirkman 1987). Young seedlings at first have an aril-like structure (Fig. 4.10e) 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. 4.10f). The mature seedling detaches from the parent plant, separates from its protecting bract, and sinks to the sea floor. The buoyant bracts of *T. pachyrhizum* wash onto the shore in December and January.

The embryos of *Amphibolis* and *Thalassodendron* obtain the nutrients required for seedling development directly from the parent plant through specialised transfer cells at the interface of developing seed and the parent tissue (Fig. 4.10g–i). Unlike seeds of other seagrasses, seedlings of these two groups of plants do not store starch.

Also in the Hydrocharitaceae, *Enhalus* bears solitary female flowers on a long peduncle reaching water surface, and enclosed by two alternates bracts; each flower has three sepals and petals. Male flowers occur in short-pedunculate inflorescences, each flower consisting of six tepals and three stamens. The mature pollen grains are released from the anthers and pollination takes place at the water surface. The fertilized female peduncle becomes helically twisted and is withdrawn from the water surface. The fruit of *Enhalus* is a fleshy capsule *ca*. 6 cm long with a spinous surface; the capsule dehisces to release the few angular seeds (Figs. 4.1d, 4.9k). The embryo has a large hypocotyl, but the radicle is not developed.

In *Thalassia*, the female flower is usually solitary on a long peduncle, with a separate spathe and three tepals, while each male flower has three tepals and many sessile stamens. The fruit of *Thalassia* is globose, containing several angular seeds (Fig. 4.9l, m); the embryo has a large hypocotyl fused with the cotyledon (Fig. 4.9n).

Most *Halophila* species are dioecious, the exceptions being *H. decipiens* and *H. capricorni*, which are monoecious. However, both male and female floral shoots of *H. decipiens* are produced from the same rhizome nodes (Kuo and Kirkman 1995, *see* also Fig. 4.8j), while either male or female floral shoots of *H. capricorni* are formed on separate rhizome nodes of the same plants (Larkum 1995). Flowers of all *Halophila* species are unisexual and enclosed by two overlapping spathes (bracts).

In the species with erect stems *H.*, e.g. *tricostata* and *H. spinulosa*, 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, *see* also Fig. 4.1b). For those species without erect stems, e.g. *H. ovalis* and *H. decipiens*, etc., flowers develop and mature progressively at each node along the rhizome branches, resulting 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 (Fig. 4.8l), then the tepals open to release pollen from the anthers. *Halophila* has ellipsoid to spherical pollen grains forming chains within mucilage tubes, up to 80 μm long, to achieve the same effect as filamentous pollen in the remaining seagrass genera (Pettitt and Jermy 1975). The female flower has a gynoecium with inferior ovary containing several to numerous ovules, 2–6 filiform styles (Fig. 4.8k) and a ring-like perianth.

The fleshy capsule of *Halophila* has a persistent ovary and contains several to numerous sub-spherical seeds, 0.5–2 mm in diameter depending on the species (Fig. 4.9p). Each seed possesses an embryo with a distinct leaf primordium protected by a coiled cotyledon, and an enlarged hypocotyl (Fig. 4.9p). The surface of the seed coat has distinct isometric reticulation in most of the *Halophila* species (Fig. 4.9j) (Kuo and Kirkman 1992, 1995) but has numerous fine protrusions in *H. tricostata* (Kuo et al. 1993).

The detailed morphological development of *Halophila* seedlings has been described in detail for *H. spinulosa* (Birch 1981); *H. decipiens* (McMillan 1988; Kuo and Kirkman 1995); and *H. tricostata* (Kuo et al. 1993). 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. A similar phenomenon also occurs in *Zostera muelleri* (Stanfford-Bell et al. 2016), some fresh water monocotyledonous and dicotyledonous seedlings (Kaul 1978), and in a few terrestrial plants (Arber 1925).

## 4.15 Concluding and Recommendations for Future Studies

This chapter illustrates the morphology and anatomy of vegetative and reproductive organs in different seagrass taxonomic groups, demonstrating that basic plant organs are similar to those of terrestrial and freshwater plants. Pollination by hydrophily is unique to the seagrasses, with specialised pollen walls lacking the rigid exine present in land plants. Different taxonomic groups of seagrass vary considerably in morphology and anatomy, reflecting an evolutionary history from several ancestral lines at different geological periods.

The chapter shows that there have been few anatomical and structural studies on seagrasses in the last decades and there is a dearth of work on vegetative and reproductive development. Examples where the lack of study are hampering our understanding of function include aspects of photosynthetic pathways in chloroplasts, how cell plasma membranes exclude excess sodium, or how filamentous pollen attaches and germinates on the receptive female stigma.

The changes in morphology and anatomy that must have evolved progressively as plant species migrated into new habitats are likely to have been accompanied by substantial modifications in the structure of organs, tissues and cells. Identifying these evolutionary responses to selection pressures provides an exciting challenge to marine biologists, especially those interested in plant structure and function but should not be carried out in isolation from physiological, biochemical and ecological investigations. Structural and developmental information could provide the basis for making progress in understating the evolution, phylogeny, biogeography and ecology of seagrasses.

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# Part III
# Molecular and Taxonomic Studies

# Chapter 5
# Systematics and Evolution of Australian Seagrasses in a Global Context

**Michelle Waycott, Edward Biffin and Donald H. Les**

**Abstract** Seagrasses have evolved independently at least four times throughout their evolutionary history. All seagrasses are members of the monocot order *Alismatales*. A new molecular phylogenetic analysis, applying a molecular clock based on recently redefined fossil evidence, provides a framework for describing the timing and relationships of seagrass lineage evolution. The deeper time phylogenetic history of the marine monocotyledons dates back approximately 105 million years ago (Ma) to an ancestor from which two significant lineages evolved more recently. The marine *Hydrocharitaceae* (*Enhalus*, *Thalassia* and *Halophila*) are a tropical globally distributed lineage which include Australian endemic species of *Halophila*. The *Cymodoceaceae* lineage and the *Zosteraceae*/*Potamogetonaceae* diverged some ~67 Ma but in each lineage the genera arose more recently. Most seagrass species appear to have evolved in the last ~5 Ma, some more recently. The extant distribution of species will not be the result of vicariance but of long distance connectivity at a global scale. The most significant implication of these

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results to global biogeography is that there must have been, and likely continues to be, ongoing long distance dispersal leading to the current widespread distributions of species and congeners. The Australian seagrass flora represents all the major evolutionary lineages of seagrasses except the northern hemisphere *Phyllospadix*, a major clade of *Zostera* and some of the forms of *Halophila*. Pollination efficiency is a significant potential driver in the evolution of filiform pollen, and is likely associated with the single seeded fruit in water pollinated species of seagrass in the lineages of seagrass that exhibit this character.

## 5.1 Introduction

Seagrasses are a biological group comprised of submerged, aquatic, marine flowering plants (Arber 1920; den Hartog 1970; Les et al. 1997). They share a broad environmental niche and are derived from multiple evolutionary lineages, i.e. they are polyphyletic (Les et al. 1997). All seagrasses are monocotyledons and occur within the predominantly aquatic plant order *Alismatales* R. Br. ex Bercht. & J. Presl (sensu APG IV, Byng et al. 2016). Some 70 species are presently recognised from thirteen genera and across six families (den Hartog 1970; Kuo and den Hartog 2006; Les 1988; Les et al. 1997; Les and Haynes 1995; Les and Tippery 2013; Waycott and Les 2000; Waycott et al. 2006; Larkum et al. 2016, this volume). Most seagrasses have wide geographic ranges, often traversing the breadth of contiguous ocean systems such as the tropical Atlantic, temperate Atlantic, the northern Pacific, and the Indo-West Pacific (den Hartog 1970; den Hartog and Kuo 2006; Green and Short 2003; Les et al. 2003; van Tussenbroek et al. 2010; Waycott et al. 2004, 2014). Many genera have congeners in adjacent ocean systems the major continental land masses representing significant barriers to larger scales of connectivity (see Larkum et al. 2016, Chap. 1). However, the origins of most modern seagrass lineages do not appear to be as closely tied to vicariance associated with continental drift (Les et al. 2002; Olsen et al. 2004), but more modern processes including long distance dispersal.

### *5.1.1 Seagrasses—A Biological Group*

There has been ongoing discussion in the literature regarding which features should define seagrasses as a biological group, with varied opinions expressed (Arber 1920; den Hartog 1970, 1971; Les et al. 1997; Waycott et al. 2006). The connection of this group to the ‘sea’ is important, because plants that simply are tolerant of 'salty water' (i.e., halophytes; Waisel 1972), will not experience the same evolutionary constraints. However, there are several seagrass features that appear consistently among the different classifications of this biological group such that:

1. Seagrasses are flowering plants, i.e. angiosperms;
2. They are tolerant for extended periods, to fully submerged marine salinities of around 35 parts per thousand total salt concentration (most oceanic salt is in the form of sodium chloride [i.e. NaCl] but the ratio of different salts may vary);
3. They complete their entire life cycle under or, in specific cases, on the surface of water, including sexual reproduction (pollination), seed germination and establishment, and shoot/rhizome and root development and growth;
4. Seagrass plants remain flexible in the water column and almost always lack secondary thickening of leaves or stems;
5. Seagrass shoots are able to remain attached to the benthic substrate for the majority of their life-history;
6. They are able to acquire all fundamental resources ($CO_2$, macro- and micro-nutrients, and metabolic $H_2O$) directly from the water column or from the sediments in which they grow.

In this review, we include thirteen genera in our discussion of seagrass systematics and evolution (Table 5.1). In an influential treatment of seagrass taxonomy, den Hartog (1970) provided the foundation for the majority of taxonomic and evolutionary work that followed. The publication of the first molecular phylogeny, based on the chloroplast gene *rbc*L, included a large proportion of seagrass taxa and a number of their freshwater relatives (Les et al. 1997). This seminal work provided new insights into the polyphyletic origin of seagrasses and generated the first data-driven evolutionary hypotheses about the number of origins of the marine (seagrass) habit, underwater pollination (hydrophily) and types of sexual systems. All of these traits were found to have evolved more than once including four different lineages containing the marine habit (Les et al. 1997; Waycott et al. 2006). More recent studies (Les and Tippery 2013; Li and Zhou 2009; Iles et al. 2014, 2015; Ross et al. 2016) have added more sequence data and included additional taxon sampling, but the main conclusions have remained consistent with those of Les et al. (1997). Here we review this earlier work and present an updated molecular phylogeny for the *Alismatales*—with emphasis on seagrasses—including divergence times based on a fossil calibrated molecular clock. We then discuss origins and distribution with a focus on the world and in particular the origin and place of Australia's seagrass flora.

**Table 5.1** Genera and their families recognised in this review as 'seagrasses'

| Family | Seagrass genus | Recognised number of species each genus[b] |
|---|---|---|
| *Hydrocharitaceae* | *Enhalus* Rich. | 1 |
| | *Thalassia* Banks ex K.D. Koenig | 2 |
| | *Halophila* Thouars | 20 |
| *Cymodoceaceae* | *Cymodocea* K.D. Koenig | 4 |
| | *Thalassodendron* Hartog | 2 |
| | *Amphibolis* C. Agardh | 2 |
| | *Syringodium* Kütz. | 2 |
| | *Halodule* Endl. | 6 |
| *Ruppiaceae* | *Ruppia* L. | 8 |
| *Posidoniaceae* | *Posidonia* K.D. Koenig | 9 |
| *Potamogetonaceae* (including *Zannichelliaceae* per APG IV) | *Lepilaena* J. Drum. ex Harv. | 6 |
| *Zosteraceae* | *Phyllospadix* Hook. | 6 |
| | *Zostera* L.[c] | 16 |
| Total | | 84 |

All groups belong to the monocot plant order *Alismatales*[a] Dumortier (Angiosperm Phylogeny Group, 2016, see below). Families containing seagrasses recognised in the order and genera currently circumscribed within each family

[a] This order will be referred to as the 'alismatid monocots' monocots' or *Alismatales*, for alternative discussions see Les and Tippery (2013) and APG IV (Byng et al. 2016)

[b] The number of species in each genus is listed by the number recognised as *valid* taxonomic names in *The Plant List* (2013). Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed 10 June 2016). These numbers may have changed in *The Plant List* as taxonomic revisions and synonymy since 2012 will be incomplete

[c] *Zostera* here includes *Heterozostera* (Setch.) Hartog per Les and Tippery (2013), *The Plant List* (2013) and Jacobs et al. (2006). An alternative model presented by several authors recognizes three genera including the results of Coyer et al. (2013) would recognise *Zostera*, *Nanozostera* and *Heterozostera* (see the Appendix). These genera represent the substantive phylogenetic lineages of their analysis. We concur these lineages represent significant evolutionary diversity. Taxonomic work to further confirm the generic concepts with well supported morphological traits to provide a practical taxonomy for this family is warranted

## 5.2 Systematics of the Alismatid Monocots

The depth of understanding of the relationships among alismatid monocots has improved steadily since the study of Les et al. (1997). In particular, greater resolution has been achieved through the addition of new nuclear and plastid gene regions, and indeed whole chloroplast genomes, for the alismatid monocots

(Les and Tippery 2013; Petersen et al. 2016; Iles et al. 2013; Ross et al. 2016). A recent comprehensive revision of the systematics of the alismatid monocots by Les and Tippery (2013) summarised the systematic information for the group that was available at that time. Their review presented a revised overview of family and genus relationships. Among their conclusions was that *Ruppia* should be included in an expanded concept of the *Cymodoceaceae*, and that *Posidonia* should be regarded as the sister group to the remainder of the *Cymodoceaceae*, but as a separate, monogeneric family (i.e. *Posidoniaceae*). Many freshwater taxa belonging to the alismatid monocots (circumscribed in the subclass *Alismatidae*) were also included in the review of Les and Tippery (2013) who also noted the unstable positions of the *Araceae* and *Tofieldiaceae* with the subclass. Since their review the orders and families in the angiosperms have been updated by the Angiosperm Phylogeny Group in their fourth revised system (i.e. APG IV, Byng et al. 2016) which also included an updated taxonomy. The APG IV update of the *Alismatales* includes fourteen families, six of which contain seagrasses (bold in list below), only three of which are entirely marine*:

1. *Araceae* Juss.
2. *Tofieldiaceae* Takht.
3. *Alismataceae* Vent.
4. *Butomaceae* Mirb.
5. ***Hydrocharitaceae*** Juss.
6. *Scheuchzeriaceae* F. Rudolphi
7. *Aponogetonaceae* Planch.
8. *Juncaginaceae* Rich.
9. *Maundiaceae* Nakai
10. ***Zosteraceae**** Dumort.
11. ***Potamogetonaceae*** Bercht. & J. Presl
12. ***Posidoniaceae**** Vines
13. ***Ruppiaceae*** Horan.
14. ***Cymodoceaceae**** Vines

Placing this revised family structure in an historical context of other family level seagrass affinities (i.e. which genera are found within each of the families: Table 5.2), demonstrates that consistency of taxonomic placement across families has emerged with only minor amendments (Table 5.2). Another feature evident from the APG IV system is the uncertain placement of monogeneric family lineages (e.g. *Maundiaceae*). It is likely that there have been numerous losses of whole lineages, and that marine lineages have been the most affected.

**Table 5.2** 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 (1985) | Thorne (1992) | Les et al. (1997) | Les and Tippery (2013) | APG IV (Byng et al. 2016) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Enhalus* | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD |
| *Halophila* | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD |
| *Thalassia* | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD | HYD |
| *Amphibolis* | POT | POT | ZAN | POT | CYM | CYM | CYM | CYM | CYM | CYM | CYM |
| *Cymodocea* | POT | POT | ZAN | POT | CYM | CYM | CYM | CYM | CYM | CYM | CYM |
| *Halodule* | POT | POT | ZAN | POT | CYM | CYM | CYM | CYM | CYM | CYM | CYM |
| *Heterozostera* | – | – | ZOS | POT | ZOS | ZOS | ZOS | ZOS | ZOS | –[b] | –[b] |
| *Lepilaena*[a] | POT | – | ZAN | – | ZAN | ZAN | ZAN | ZAN | ZAN | POT | POT |
| *Phyllospadix* | POT | POT | ZOS | POT | ZOS | ZOS | ZOS | ZOS | ZOS | ZOS | ZOS |
| *Posidonia* | POT | POT | POS | POT | POS | POS | POS | POS | POS | POS | POS[c] |
| *Ruppia* | POT | POT | RUP | POT | RUP | POT | POT | POT | RUP | CYM | RUP[c] |
| *Syringodium* | POT | – | ZAN | POT | CYM | CYM | CYM | CYM | CYM | CYM | CYM |
| *Thalassodendron* | POT | – | – | POT | CYM | CYM | CYM | CYM | CYM | CYM | CYM |
| *Zostera* | POT | POT | ZOS | POT | ZOS | ZOS | ZOS | ZOS | ZOS | ZOS | ZOS |

*CYM* Cymodoceaceae; *HYD* Hydrocharitaceae; *POS* Posidoniaceae; *POT* Potamogetonaceae; *RUP* Ruppiaceae; *ZAN* Zannichelliaceae; *ZOS* Zosteraceae. – included elsewhere (in synonymy) or not considered by author. Table expanded from Waycott et al. (2006)

[a] Not always accepted as 'seagrasses', but included as a marine lineage in the *Zannichelliaceae* (Les et al. 1997)

[b] Currently included within *Zostera* (Jacobs et al. 2006; Les and Tippery 2013)

[c] Note the family was retained in the APG IV treatment although recognition of several small families in a series led to survey conducted by the plant systematics community in 2014 (Royal Botanic Gardens, Kew, survey closed 31 August 2014) to gain support for maintaining separate families or combining into larger groups, the consensus was to maintain these families at this time

## 5.3 Molecular Phylogenetics of Alismatid Monocots

A recent analysis of complete chloroplast genome sequences of the alismatid monocots (Ross et al. 2016) has improved the resolution of the backbone (sometimes referred to as the 'stem' group) of *Alismatales* relationships. Among the seagrass families, resolution and support for relationships outlined in Les et al. (1997) were confirmed by the expanded 83 plastid genes represented in the whole chloroplast analysis (Ross et al. 2016). Consistent among all analyses was that the taxonomic groups accepted as seagrasses (see above) are derived from four lineages (Les et al. 1997; Les and Tippery 2013; Li and Zhou 2009; Petersen et al. 2016; Ross et al. 2016). These lineages are:

- A marine group of the *Hydrocharitaceae*, including *Enhalus*, *Halophila* and *Thalassia*;
- The members of the traditionally circumscribed *Cymodoceaceae* (*Halodule*, *Syringodium*, *Thalassodendron*, and *Amphibolis*), along with the monogeneric families *Ruppiaceae* and *Posidoniaceae*, which has been referred to as the *Cymodoceaceae* 'complex' by Les et al. (1997);
- The *Zosteraceae* comprised of *Zostera* (including *Heterozostera* and *Nanozostera* following Coyer et al. (2013)) and *Phyllospadix*;
- A few species of *Lepilaena* in the *Potamogetonaceae* (previously in the segregate family *Zannichelliaceae*).

Further insight into the evolutionary origins, diversification and adaptation of seagrasses, requires each lineage to be evaluated independently. Features shared across lineages may be the consequence of a shared, deeper ancestry with a freshwater ancestor or as a result of convergent evolution through parallel adaptation to similar environmental conditions.

### *5.3.1 Molecular Clock Estimates of Divergence Times for Seagrasses*

Phylogenetic reconstructions are now widely used to evaluate the historical divergence times among lineages (Bromham and Penny 2003; Kumar and Hedges 2016). The use of molecular clock analysis involves assumptions that must be applied with regard to error in the fossil record and estimates of mutation rates of the genes used (e.g. Kumar and Hedges 2016; dos Reis et al. 2016) Nevertheless, used cautiously, molecular clocks provide additional insights that cannot be gained any other way. In seagrasses and other alismatid monocots, several studies have applied molecular clock estimates to phylogenies to investigate a range of lineage-specific questions (Chen et al. 2013, 2015; Coyer et al. 2013; Janssen and Bremer 2004; Les et al. 2003).

Prior to the availability of molecular clock estimates, it was assumed that the majority of extant seagrass and freshwater relatives arose vicariantly (Wiley 1988; Morrone and Crisci 1995; Ronquist 1997), i.e. as a consequence of long-term isolation on the scale of geological epochs (den Hartog 1970; den Hartog and Kuo 2006; Larkum and den Hartog 1989). Given the oceanic scale of seagrass species distributions (den Hartog 1970; den Hartog and Kuo 2006; Green and Short 2003; Larkum and den Hartog 1989; Larkum et al. 2016; Waycott et al. 2006), an inference of vicariance was appropriate; however, one consequence of this interpretation was that it necessarily assumed that long distance (i.e. global scale) dispersal was very limited or virtually impossible (den Hartog 1970). Our understanding of long distance seagrass dispersal has improved as a result of ecological and genetic studies (Kendrick et al. 2012; McMahon et al. 2014; van Dijk et al. 2009). It is now evident that dispersal scales are much greater than previously assumed and that credible mechanisms exist for the potentially expansive movement of vegetative and reproductive seagrass propagules (Kendrick et al. 2012; McMahon et al. 2014).

In a study of paired congeneric aquatic species disjunctions, Les et al. (2003) demonstrated that a revised or theoretical context for extant species distributions was necessary. Les et al. (2003) calculated divergence times between sister species of aquatic plant, including seagrasses, which were distributed over different continents. The pairs of seagrass species compared by Les et al. (2003) were *Posidonia australis* and *P. oceanica*, *Zostera muelleri* and *Zostera noltei*, *Thalassia hemprichii* and *T. testudinum*, *Syringodium isoetifolium* and *S. filiforme* and the closely related genera *Lepilaena* and *Zannichellia*, (Table 5.3). They also compared other species pairs from the *Alismatales*, as well as more distantly related groups such as *Callitriche*, *Myriophyllum*, *Lemna* and *Wolffia*. Les et al. (2003) generated their proposed divergence times using the substitution rates of various DNA sequences. Divergence times (Table 5.3) in *Zostera* ranged from 21.4 (±7.9) Ma (million years ago) for *Zostera muelleri* and *Z. marina* (Australia to USA) to 2.8 (±1.3) Ma for *Zostera muelleri* (syn. *capricorni*) and *Z. noltei* (syn. *noltii*) (Australia to Mediterranean). A greater divergence time was estimated between the estuarine *Lepilaena* in Australia and *Zannichellia* from North America. Although these genera are regarded as relatively closely related, their divergence time was estimated to be fairly long (38.3 Ma). Other studies that have applied molecular clock estimates to seagrasses (e.g. Chen et al. 2013; Coyer et al. 2013, Table 5.3) also have applied a substitution rate model to generate time calibrated phylogenies.

Here we present an updated phylogenetic analysis of the *Alismatales* based upon DNA sequences including divergence time estimates inferred using an array of accepted monocotyledon fossils to calibrate mutation rates. The choice of suitable fossils is critical to accurate calibration. Because putative seagrass fossils remain controversial, we excluded them and utilized non-disputed fossils of other alismatids following Iles et al. (2015) and Hertweck et al. (2015). The results of these analyses are then used as a basis to review the evolutionary history of seagrass lineages.

**Table 5.3** Molecular clock, substitution rate and fossil calibrated divergence times, estimated for pairs of seagrass species or taxon groups, in three different studies (Chen et al. 2012; Coyer et al. 2013; Les et al. 2003)

| Taxon comparison 1 | Taxon comparison 2 | Divergence time (Ma)[a] |
|---|---|---|
| Study 1 | Les et al. (2003) | Congener pairs |
| **Australia** | **Mediterranean (seagrasses)** | |
| *Posidonia australis* | *Posidonia oceanica* | 16.7 (±12.3) |
| *Zostera muelleri* (syn. *capricorni*) | *Zostera noltei* (syn. *noltii*) | 2.8 (±1.3) |
| **Australia** | **North America** | |
| *Lepilaena* | *Zannichellia* | 38.3 (n.a.) |
| *Zostera muelleri* (syn. *capricorni*) | *Zostera marina* | 21.4 (±7.9) |
| *Thalassia hemprichii* | *Thalassia testudinum* | 14.6 (n.a.) |
| *Syringodium isoetifolium* | *Syringodium filiformis* | 5.8 (n.a.) |
| **Study 2** | Chen et al. (2012) | *Hydrocharitaceae* |
| *Halophila* (all spp.) | *Thalassia/Enhalus* | 19.41 (4–16[b]) |
| *Halophila engelmannii* (Atlantic) | *Halophila ovalis* (Indo-West Pacific) | 18.59 (9–33[b]) |
| *Enhalus acoroides* | *Thalassia spp.* | 8.04 (5–26[b]) |
| *Thalassia testudinum* | *Thalassia hemprichii* | 0.98 (0–2.5[b]) |
| Marine Hydrocharitaceae | Non-Marine Hydrocharitaceae | 50.84 (45–70[b]) |
| **Study 3** | Coyer et al. (2013) | *Zosteraceae* |
| *Zostera* | *Phyllospadix* | 23.27 (7–60[b]) |
| *Zostera marina* clade (i.e. Clade II) | *Zostera muelleri/Z. japonica* clade (i.e. Clade III) | 14.44 (3–46) |
| *Zostera muelleri/Z. japonica* clade (i.e. Clade III) | *Zostera tasmanica* clade (i.e. *Heterozostera* clade, Clade IV) | 6.35 (1–25) |
| *Zostera polychlamys* | *Z. tasmanica* (including other species) | 2.26 (0–10) |

Note current nomenclature used with synonymy in parentheses

[a] Estimates of confidence presented either as Study 1. ±SD (Les et al. 2003), Study 2. as the 95% confidence intervals (Chen et al. 2012), and Study 3. as the 95% Highest Probability Density (Coyer et al. 2013)

[b] 95% HPD estimated from Fig. 5.1 in Chen et al. (2012) or Fig. 6 in Coyer et al. (2013)

### 5.3.2 *A Molecular Clock-Based Phylogenetic Analysis for* **Alismatales** *with an Emphasis on Seagrass Lineages*

Phylogenetic relationships and divergence time estimates were inferred using two chloroplast DNA gene regions, *rbcL* and *matK*, and included seagrass lineages and outgroups sourced from GenBank (Table 5.5). The sequences for each gene were aligned separately using the Muscle plugin for GENEIOUS v8.15 (Kearse et al. 2012) with default parameters and were subsequently concatenated. Phylogenies were estimated using Bayesian (BEAST package v2.3 Bouckaert et al. 2014) and Maximum Likelihood methods (PhyML as implemented in the Geneious plugin 'PhyML'; Guindon et al. 2010).

In BEAST, phylogeny and divergence times were estimated using the fossilised birth-death model (Gavryushkina et al. 2014), which imposes a time structure on the tree, while accounting for uncertainty in the placement of the fossil data by allowing all plausible placements for the fossil taxon on the extant tree (Heath et al. 2014). We used six fossil constraints and following Hertweck et al. (2015), we adopted constraints on the *Araceae* (120–116 Ma 95% CI), *Arecales* (75–67 Ma), *Poaceae* (72–65 Ma), *Schisandraceae* (81–77 Ma) and *Zingerberales* (72–68 Ma) stem groups, and the *Pandanales* (91–87 Ma) crown group (calibrations 7, 9, 11, 2, 10 and 8, respectively, in Hertweck et al. 2015). We forced the monophyly of each of these groups along with the fossil observation, but placed no further restriction on the placement of each fossil within its associated lineage. Additionally, placed a constraint on the origin (root) age of 150 Ma (c. 120–180 Ma, 95% confidence interval), in line with fossil based estimates for the age of the angiosperm radiation (e.g. Beaulieu et al. 2015). For the BEAST analyses we modelled branch rates using an uncorrelated relaxed molecular clock and a general time reversible (GTR) substitution model with gamma rate heterogeneity to model sequence evolution. We ran four independent chains over 50 million steps, and, after excluding the appropriate burn-in fraction, used LOGCOMBINER and TREEANNOTATOR (both part of the BEAST package) to produce a summary of the four runs.

The PHYML analyses used a GTR (general time reversible) model of sequence evolution along with a gamma rate distribution and the model parameters, along with the proportion of invariant sites, were estimated from the data. Clade support was assessed on the consensus topology built from a non-parametric bootstrapping approach using 1000 pseudoreplicates.

The results of the molecular dating analyses are shown in Figs. 5.1 and 5.2. Groups of species associated with a particular node are collapsed into terminal 'triangles' to facilitate readability, and all nodes referenced in the text are annotated with a lower case letter (Figs. 5.1 and 5.2). A summary of resulting estimated divergence times for these nodes is provided (Table 5.4). For comparative purposes, the *Alismatales* phylogenetic analysis also is presented as a consensus PhyML tree depicting all nodes with greater than 50% bootstrap support. It is important to note that there are several approaches used to interpret estimates of chronological lineage ages. Here we adopt the approach that we refer to as the "mean node age", but endeavour to refer to the range of molecular clock estimated ages as the confidence interval (i.e. 95% Highest Probability Density). Note that these data are based on DNA sequences for cpDNA regions that have been well characterised for their use in molecular clock estimates.

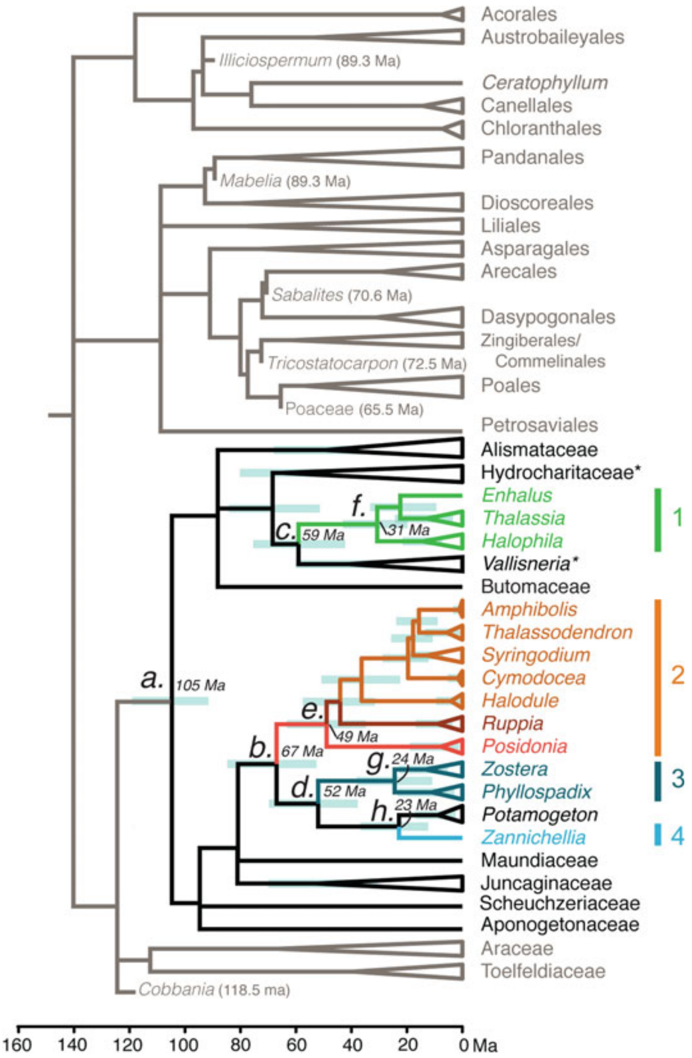


**Fig. 5.1** Time-calibrated phylogenetic relationships among the *Alismatales* and other moncotyledon groups based on *rbc*L and *mat*K cpDNA sequences. The 95% Highest Probability Density (i.e. confidence interval) is indicated by a shaded bar for each node. The scale bar at the base of the figure represents the fossil calibrated time as millions of years (Ma). Only the nodes having $\geq 85\%$ posterior probability support or bootstrap support were retained (latter not shown); all others were collapsed to the next most strongly supported node. Groups of species from particular lineages are collapsed into terminal ‘triangles’ to facilitate readability, and nodes referred to in the text are annotated with a lower case letter (a–h). Numbers to the right indicate clades (see Fig. 5.2 for more detail)

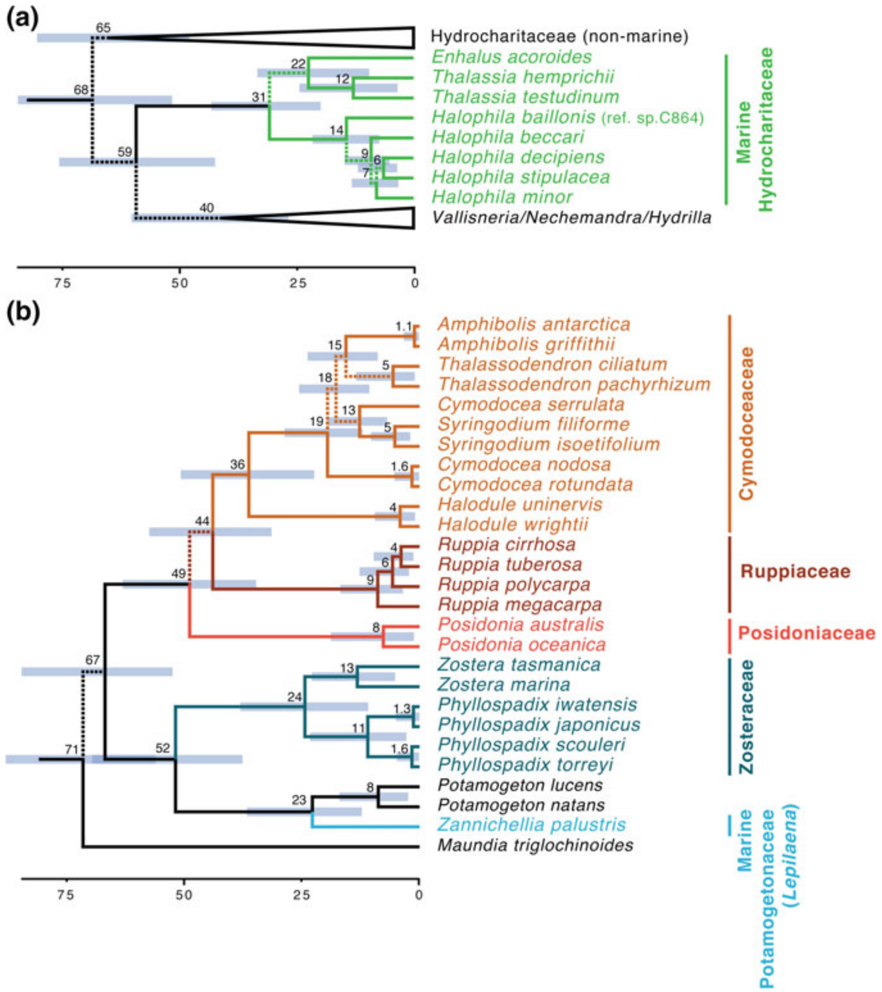


**Fig. 5.2** Time-calibrated phylogenies for the seagrass lineages within the *Alismatales* based on *rbc*L and *mat*K cpDNA sequences. The 95% Highest Probability Density (i.e. confidence interval) is indicated by a shaded bar along each node. Values above nodes are the estimated divergence time for that node. Solid lines indicate $\geq 85\%$ support; dotted lines <85% support. Colours of seagrass lineages are the same as in Fig. 5.1. GenBank source of data can be found in Appendix 1

**Table 5.4** Molecular clock estimates of time-calibrated divergence times for reference points identified in Fig. 5.1

| Divergence event | Node label on Fig. 5.1 | Divergence time estimate, Ma | Confidence interval[a] |
|---|---|---|---|
| Ancestral node i.e. seagrasses diverged from remainder of alismatid monocots | a. | 105 | 119–92 |
| *Cymodoceaceae* diverge from *Zosteraceae/Potamogetonaceae* | b. | 67 | 88–56 |
| Marine *Hydrocharitaceae* from other *Hydrocharitaceae* | c. | 59 | 75–42 |
| *Zosteraceae* and *Potamogetonaceae* diverge | d. | 52 | 70–38 |
| *Posidonia* separates from other *Cymodoceaceae* 'complex' (*Cymodoceaceae* and *Ruppiaceae*) | e. | 49 | 68–35 |
| *Halophila* diverges from *Thalassia/Enhalus* in marine *Hydrocharitaceae* | f. | 31 | 43–20 |
| *Zosteraceae* diverges into *Phyllospadix* and *Zostera* | g. | 24 | 38–11 |
| *Lepilaena* (cf. *Althenia*) i.e. '*Zannichelliaceae*' diverges from remaining *Potamogetonaceae* | h. | 23 | 37–12 |

Estimates are presented as million years ago (Ma) and were generated in BEAST (v2.3 Bouckaert et al. 2014)

[a] Confidence interval presented as 95% highest posterior density

## 5.4 Marine Lineages of the *Alismatales*

Our phylogenetic analysis of *Alismatales* based on combined *rbcL* and *matK* sequences supports previous findings of non-monophyly of the marine lineages. However, our molecular clock estimates provide greater resolution, especially with respect to the origins of the four seagrass lineages (Fig. 5.1) and genera (Figs. 5.2 and 5.3) in a deeper time frame. The four marine lineages are numbered in Fig. 5.1 and mean divergence times are used in the discussion below.

Lineage 1: A monophyletic marine lineage in the aquatic family *Hydrocharitaceae* ~31 Ma. *Enhalus* appears to be the most ancestral (~22 Ma) with *Thalassia* (~12 Ma) and *Halophila* (~14 Ma) more recently derived. *Enhalus* is restricted to the Indo West Pacific, *Halophila* is found in tropical waters globally with some incursions into temperate waters, most notably *Halophila australis* in southern Australia, *Thalassia* is throughout the tropics globally.

Lineage 2: A major radiation of globally distributed seagrasses (including *Cymodoceaceae*, *Ruppiaceae* and *Posidoniaceae*) which is referred to as the *Cymodoceaceae* lineage. This whole lineage arose ~49 Ma the families *Cymodoceaceae* sensu stricto (~44 Ma), *Ruppiaceae* (~9 Ma) and *Posidoniaceae*

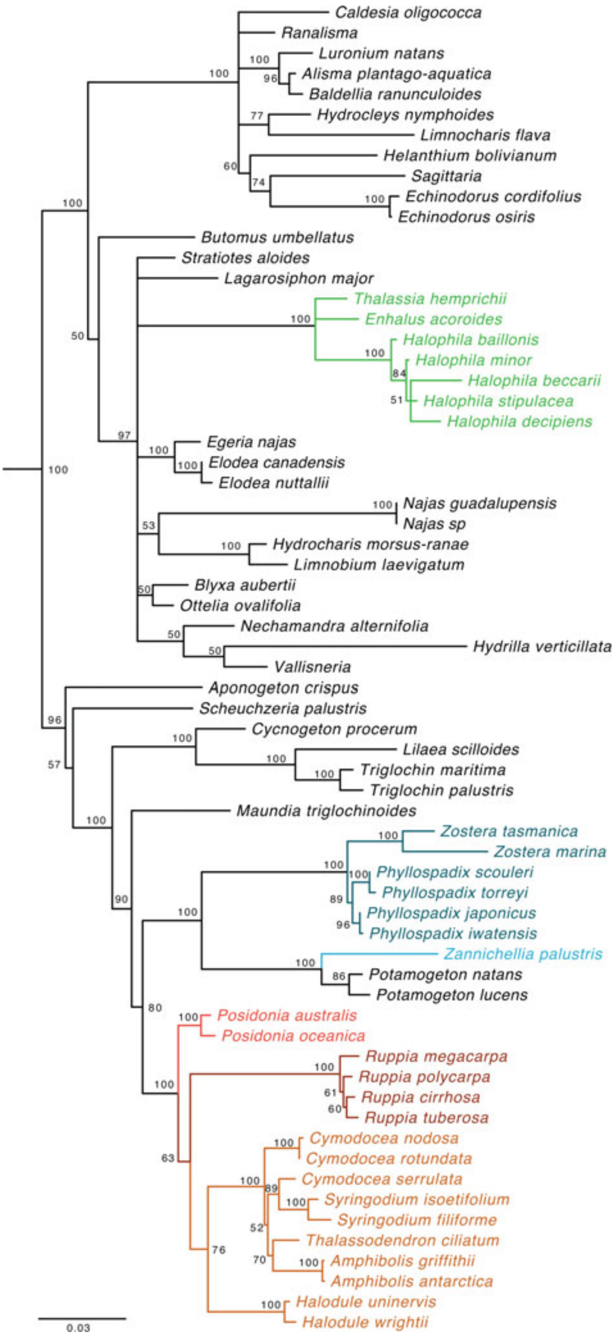


**Fig. 5.3** Phylogenetic consensus tree for *Alismatales* (inclusive of taxa from reference point a. in Fig. 5.1) based on *rbc*L and *mat*K cpDNA sequences generated in PHyML. Nodes with $\geq 50\%$ bootstrap support are marked. Colours of seagrass lineages are equivalent those used in Figs. 5.1 and 5.2. Genbank source of data can be found in Appendix 1

(~8 Ma). While the ancestral lineage is old, the extant genera and species are recently evolved (all <13 Ma).

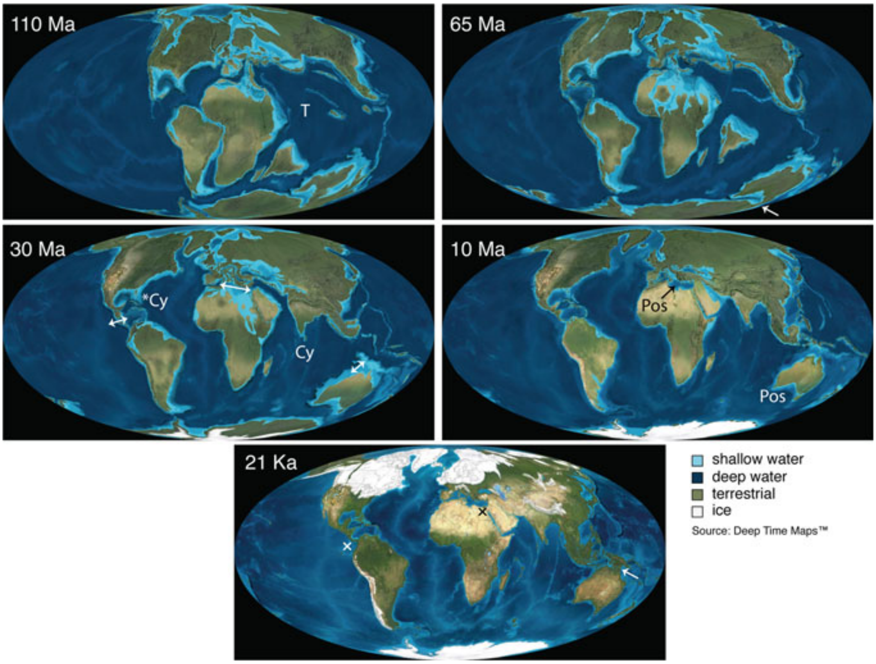
Lineage 3: A strongly supported *Zosteraceae lineage*, which is more diverse in the northern hemisphere and sister to the *Potamogetonaceae*. The *Zosteraceae* diverged ~24 Ma and the *Potamogetonaceae* ~23 Ma, their most recent common ancestor having arisen ~52 Ma. Again, the extant species of *Zostera* are recent (~13 Ma), as is *Phyllospadix* (~11 Ma). *Zostera* is found from warm-temperate to polar latitudes. It is worth noting that *Z. marina* is by far the dominant seagrass species throughout the temperate northern hemisphere, and does not have the equivalently widespread dominant congener in the southern hemisphere although several are widespread, the Australian/New Zealand species, *Z. muelleri* in particular.

Lineage 4: A small marine *Potamogetonaceae* lineage, represented at present by a few Australian species of *Lepilaena* (and potentially others, pending additional review). The lineage diverged ~23 Ma and is predominantly freshwater (both hemispheres).

## 5.5 Origins and Characteristics of the Different Seagrass Lineages

Deep phylogenetic divergence ~105 Ma among the ancestral monocotyledons has resulted in the lineage containing all extant marine lineages of the *Alismatales*. This lineage that today contains all the seagrasses is indicated on Fig. 5.1 by node a. (confidence interval 119–92 Ma). Globally shallow water marine ecosystems were extensive at that time (Fig. 5.4, 110 Ma map). Many of the modern orders and families of flowering plants have their origins at this time as well (Soltis et al. 2005). The ancestor to the *Alismatales* is likely to have been freshwater aquatic or semi-aquatic in habit, able to tolerate regular or permanent inundation. Subsequent to this, there was separation of the *Alismatales* into two major groups, one including the marine Hydrocharitaceae, the second containing the other lineages (lineages 2–4, Fig. 5.1). These two groups have elements of their more recent histories that likely reflect global trends during certain periods, notably their stem groups were both formed around 59–67 Ma (nodes b. and c., Fig. 5.1), with the radiations into modern families occurring more recently. This implies a scenario where a significant adaptive radiation of aquatic plant groups, those entering the marine environment, was associated with the colonisation of new niches. This time period (~66 Ma, Fig. 5.4, 65 Ma map) is known as the Cretaceous–Paleogene (K–Pg) extinction event, also referred to as the KT Boundary (Schulte et al. 2010).

Evolutionary studies of the history of the angiosperms has revealed that during the K–Pg period a significant proportion of the major radiations of flowering plants occurred (Soltis et al. 2005; Bell et al. 2010). In addition, recent analyses of complete plant genomes has demonstrated that whole genome duplications occurred in a large number of angiosperm lineages (Van de Peer et al. 2009; Vanneste



Source: Deep Time Maps™

**Fig. 5.4** Palaeogeographic reconstruction maps representing global continental and ocean features for five epochs—110 million years ago (Ma), 65 Ma, 35 Ma, 10 Ma and the last glacial maximum during the Pleistocene (21,000 years ago). The relative placement of modern continents are drawn as outlines for reference. The following features are highlighted—110 MA, T = Tethys Sea; 65 Ma, arrow indicated the maintained connection between the Australian and Antarctic land masses; 30 Ma, the arrows indicate maintenance of the oceanic connectedness between North and South America, Africa and Asia and Europe and Australia and New Guinea. Cy = presence of the Cymodoceaceae in the Indo West Pacific region, *Cy = fossil evidence of the Cymodoceaceae in the tropical Atlantic, not in evidence today (Ivany et al. 1990); 10 Ma, Pos = region that today *Posidonia* species occur; 21 Ka, marks indicate the loss of oceanic connectedness at Panama, Suez and Torres Strait. Base maps provided by Deep Time Maps™ with permission

et al. 2014; Lohaus and Van de Peer 2016). Such a whole genome duplication has been observed in the recent analysis of the *Z. marina* whole genome by Olsen et al. (2016). This ground breaking observation supports the idea that at the genomic scale, adaptations to survival were extreme. Many such genome duplications have been traced to a similar time period to the global upheaval in biodiversity, i.e. the Cretaceous–Paleogene (K–Pg) boundary (Fawcett et al. 2009; Vanneste et al. 2014). The implication of these coincident observations is that an important component of evolutionary drivers leading to modern seagrass biodiversity was the result of significant new habitats opening up following the Cretaceous–Paleogene (K–Pg) extinction event (Fig. 5.4, 65 Ma map). Coupled with ongoing changing environmental conditions, a variety of environments and conditions become available for marine plants to occupy, leading to the subsequent, but more recent speciation.

Using this niche occupancy as a context, the origins of lineage 1 are likely to be a marine derived group within an otherwise freshwater aquatic *Hydrocharitaceae*. The marine lineage is derived from a transition from submerged and freshwater to submerged and increasingly salinity tolerant. In addition, plants become more able to occupy the energetic oceanic hydrodynamic environment. Sister genera to the marine group in the *Hydrocharitaceae* (~59 Ma, Fig. 5.1, node c.) share many features including an unusual surface pollination system seen in both *Vallisneria* and *Enhalus*. The earliest diverging lineage in the marine *Hydrocharitaceae* is the genus *Halophila* (~31 Ma, Fig. 5.1, node f., Fig. 5.2). *Halophila* exhibits several defining characteristics including a unique petiolate leaf form morphology, mixed breeding systems (monoecious and dioecious species). *Halophila* also has a relatively high degree of speciation, including regional endemic species such as *Halophila australis* (temperate Australia) and *Halophila trichostata* (tropical eastern Australia).

In contrast, the ancestral habit of lineage 2 (~49 Ma, Fig. 5.1, node e.), given the ubiquity of salinity tolerance in all derived linages, would likely have been a salinity tolerant, submerged aquatic plant. This lineage also represents the major radiation into tropical ecosystems in the overall group (i.e. species of *Halodule*, *Syringodium*, *Cymodocea*, *Thalassodendron*). Fossil evidence of distinctive material clearly from this lineage, in fact clearly from the Cymodoceaceae (affinities to *Cymodocea* and *Thalassodendron*) suggest that it did exist in the tropical Atlantic historically (Fig. 5.4, 30 Ma map), however they are not in evidence today (Ivany et al. 1990). The idea that there was a globally distributed ancestor to the modern lineages present in the tropical Atlantic ~25–30 Ma is consistent with our analysis, which demonstrates the derivation of the major radiation of the *Cymodoceaceae* has occurred ~36 Ma (Fig. 5.2) although *Halodule* diverged around 10 Ma earlier (Fig. 5.2). All genera in the *Cymodoceaceae* are dioecious and, with the exception of *Amphibolis*, which is an Australian endemic genus, are very widespread throughout the tropics. Given their relative recent evolutionary origins (5–15 Ma), these genera must have had the ability to disperse over long distances to have achieved their current distributions.

The shared common ancestor to lineage 3 and lineage 4 (Fig. 5.1, node d., ~52 Ma) is likely to have been an aquatic plant with the potential for salinity tolerance, although it is most likely to have been primarily adapted to freshwater. The dominant breeding system is monoecy across these two lineages and this clade (i.e. node d.) as a whole, with some dioecious groups being derived (e.g. *Zostera* is monoecious and *Phyllospadix* is dioecious). The derivation of lineage 3, the *Zosteraceae*, as a fully marine and temperate lineage (~24 Ma. Fig. 5.1, node g.), is characterised by the development of a spadix inflorescence. Lineage 4 (~23 Ma Fig. 5.1, node h.) is comprised of a few marine tolerant taxa (e.g. *Lepilaena marina*), common in temperate Australia, among a group of otherwise freshwater and brackish tolerant species and genera, including *Potamogeton*, a very large widespread aquatic plant genus.

## 5.6 Pollen Morphology, Hydrophily and Seagrass Evolution

The Core *Alismatales* may be separated into two clades (Fig. 5.1, node a.) one, a petaloid clade (which includes the marine *Hydrocharitaceae*), the other a tepaloid clade (which includes all other seagrasses) (Posluszny et al. 2000). The petaloid clade are characterised by seagrasses (i.e. the marine *Hydrocharitaceae*), which have non-filamentous pollen (i.e. spherical or elliptical/reinform). The tepaloid clade seagrasses in the other three lineages have filiform (confervoid) pollen (Ackerman 1995) in hydrophilous species. There are exceptions specifically *Ruppia* and *Lepilaena*, which are not wholly marine nor hydrophilous and they do not possess filamentous pollen. *Ruppia* pollen is elongate but not filiform (Ackerman 2006; den Hartog and Kuo 2006; Robertson 1984) and pollen grains of *Lepilaena* are spherical (Ackerman 2006; den Hartog and Kuo 2006; McConchie et al. 1982). These exceptions to pollen morphology appear to be associated with surface pollination, which both genera exhibit (Cox and Knox 1989; Les 1988). The presence of filiform pollen in different lineages supports the hypothesis of convergent pollen evolution as suggested by Ackerman (1995) and Les et al. (1997).

There may be a foundation to this convergence that relates to selection for reproductive success in hydrophilous seagrass species. Petaloid seagrasses all have many-seeded capsules for fruits. *Halophila trichostata*, for example, has up to 60 seeds per fruit (Kuo et al. 1993), *Thalassia* fewer with up to 6 seeds per fruit (den Hartog 1970) (note *Enhalus* is not hydrophilous). A large number of ovules requires numerous pollen grains to reach a stigma in order to achieve efficient pollination. In contrast, tepaloid seagrass clades all have single-seeded fruits, which require only a single pollen grain per flower. Thus, the evolution of elongated single grains, which are hydrodynamically optimal, will reflect an optimal strategy for tepaloid seagrass pollen evolution. In petaloid seagrasses, the formation of pseudofilamentous pollen vehicles has been achieved by the forming of chains of spherical pollen and when finding a stigma there are many pollen grains for the many ovules in the ovary.

### *5.6.1 Origins of the Australian Seagrasses*

The Australian seagrass flora reflects the long-term evolutionary history of the seagrasses as a whole in the *Alismatales*. The Australian continental waters only lack *Phyllospadix*, a conspicuous element of northern hemisphere Zosteraceae, along with one major lineage of *Zostera* (Clade II, Coyer et al. 2013), and some of the morphological diversity found in *Halophila*. The most striking feature of the Australian seagrass flora is its overall diversity (also discussed in Chap. 1). This includes the presence of a well developed tropical flora with all genera represented, along with nearly all temperate genera including the endemic genus *Amphibolis*. In addition there are a number of species are endemic in Australia.

The presence of endemic seagrass groups in Australia is unusual globally. The major radiations unique to Australia include for temperate systems: *Amphibolis* (2 species), *Halophila* (1 species, *H. australis*), *Zostera* (also known as *Heterozostera–Z. tasmanica*, *Z. nigricaulis* and *Z. polychlamys*), and *Thalassodendron* (*T. pachyrhizum*); for the tropics: *Halophila* (*H. trichostata*) and *Cymodocea* (*C. angustata*). A central assumption for much of the discussion on seagrass biogeography has been, until recently, that long distance dispersal would be limited or not possible. Recent reviews (Kendrick et al. 2012, McMahon et al. 2014, McMahon et al. genetic connectivity chapter) summarise the growing body of genetic evidence for scales and mechanisms of connectivity in seagrasses. Where detailed studies have been conducted, scales of connectivity among populations can be in the order of 100's to 1000's of km's (McMahon et al. genetic connectivity chapter). During the last glacial maximum (Fig. 5.4, 21 Ka map), approximately 21,000 years ago, when sea level was significantly lower than today, continental Australia was connected to New Guinea and Tasmania. The shallow coastal margins would have been narrowed and a strong west to east barrier to connectivity would have been in place. This restricted availability of habitat would have forced many species to refugia making connectivity even more important for survival.

It is only through the ability of seagrasses to disperse long distances that there is a reasonable explanation for the presence of many populations of the same species or genus at inter-continental scales. In particular, it has been difficult to explain how species of *Posidonia* can be occurring in southern Australia and in the Mediterranean. This genus is generally temperate in its environmental tolerances although does extend into some sub-tropical waters (e.g. Shark Bay). There is a diversity of species found in western and south-western Australia, extending to Tasmania and one species makes it up the Australian east coast. One species (*P. oceanica*) occurs in the Mediterranean. The molecular clock analysis we present suggests *Posidonia* species in both oceans diverged ~8 Ma, and around that time, direct connectivity was not possible by ocean (Fig. 5.4, 10 Ma map, labelled Pos on map). That would suggest an ancestor that was widespread in both regions prior to the loss of connectivity between the Mediterranean region and the Indian Ocean, sometime in the past 20 Ma.

A significant obstacle to elucidating the origins of seagrass diversity is our inability to fully understand the nature and causes of evolutionary diversification in these groups. Because the Australian seagrass flora was derived from a widespread global flora, and because many endemic seagrass species have evolved in the region, the country provides an excellent resource for the continued study of speciation mechanisms in marine flowering plants. To achieve this goal, a more sophisticated understanding of specialised adaptations in the seagrasses as a group will be necessary. Certainly the current uncertainty of seagrass taxonomy of reflects challenges faced in studying plants with unusually wide distributions, that are also are adapted to their environment at least in part due to high morphological plasticity, have highly reduced morphology, and whose reproductive traits are not well understood.

# Appendix 1

See Table 5.5.

**Table 5.5** List of samples and their GenBank numbers (ncbi.nih.gov) used in phylogenetic analysis

| Taxon | rbcL | matK |
|---|---|---|
| *Acanthochlamys* | HQ845619 | KP083039 |
| *Acorus calamus* | M91625 | AB040154 |
| *Acorus gramineus* | D28866 | AB040155 |
| *Acorus tatarinowii* | AY298815 | EU814660 |
| *Alisma plantagoaquatica* | L08759 | AB040179 |
| *Alstroemeria sp.* | Z77254 | AY624481 |
| *Amphibolis antarctica* | KF488485 | KF488499 |
| *Amphibolis griffithii* | HQ901574 | KP083060 |
| *Aponogeton crispus* | DQ859162 | KF632787 |
| *Arisaema* | AY298817 | AM920628 |
| *Austrobaileya* | L12632 | DQ401347 |
| *Baldellia ranunculoides* | HM849805 | KF632788 |
| *Barbacenia elegans* | AJ131946 | FR832731 |
| *Blyxa aubertii* | U80694 | KF632789 |
| *Borya* | Y14982 | AF542577 |
| *Butomus umbellatus* | U80685 | AY952416 |
| *Calochortus minimus* | Z77263 | KM085686 |
| *Calamus* | AJ404775 | JQ435566 |
| *Caldesia oligococca* | HQ456502 | KF632791 |
| *Calla palustris* | KF632846 | KF632782 |
| *Calochortus* | Z77263 | KP083037 |
| *Canna* | AF378763 | KP083045 |
| *Carludovica palmata* | AF197596 | AF542578 |
| *Ceratophyllum demersum* | D89473 | AJ581400 |
| *Chamaelirium luteum* | AF206749 | KP643031 |
| *Chloranthus* | L12640 | na |
| *Clintonia borealis* | AF206751 | AB024542 |
| *Cycnogeton procerum* | KF632854 | KF632824 |
| *Cymodocea nodosa* | KF488487 | KF488502 |
| *Cymodocea rotundata* | KF488489 | KF488504 |
| *Cymodocea serrulata* | KF488492 | KF488507 |
| *Dasypogon* | AY123229 | KP083042 |
| *Dioscorea* | AJ235803 | AB040208 |
| *Drimys* | AF093734 | AJ581398 (*Belliolum*) |

(continued)

**Table 5.5** (continued)

| Taxon | rbcL | matK |
|---|---|---|
| *Ecdeiocolea* | AY123235 | DQ257530 |
| *Echinodorus cordifolius* | DQ859164 | KF632792 |
| *Echinodorus osiris* | DQ859165 | KF632793 |
| *Egeria najas* | DQ859166 | KF632795 |
| *Elodea canadensis* | HQ901566 | KF632796 |
| *Elodea nuttallii* | AB004888 | AB002568 |
| *Enhalus acoroides* | AB004889 | AB002569 |
| *Freycinetia* | AF206770 | AB040209 |
| *Gymnostachys anceps* | M91629 | AB040177 |
| *Halodule uninervis* | KP739815 | KP739817 |
| *Halodule wrightii* | JN225357 | JN225379 |
| *Halophila baillonis (ref. sp. C864)* | DQ859168 | na |
| *Halophila beccari* | JX457599 | JX457606 |
| *Halophila decipiens* | JX457598 | JX457605 |
| *Halophila ovalis (ref. minor)* | JN225347 | JN225367 |
| *Halophila stipulacea* | JN225356 | JN225381 |
| *Helanthium bolivianum* | KF632848 | KF632794 |
| *Heliconia* | AF378765 | JQ435568 |
| *Hemerocallis* | FJ707502 | AJ581422 |
| *Heterozostera tasmanica* | U80730 | AB096171 |
| *Hydrilla verticillata* | AB004891 | AB002571 |
| *Hydrocharis morsus ranae* | HQ901567 | KF632801 |
| *Hydrocleys nymphoides* | AB004900 | AB002580 |
| *Illicium* | L12652 | AF543738 |
| *Kingia* | AY123232 | AM114718 |
| *Lagarosiphon major* | U80703 | KF632803 |
| *Lilaea scilloides* | U80715 | KF632804 |
| *Lilium superbum* | L12682 | AB040200 |
| *Limnobium laevigatum* | AB004894 | AB002574 |
| *Limnocharis flava* | JF781048 | JF781075 |
| *Luronium natans* | U80680 | JN894192 |
| *Maundia triglochinoides* | HQ901577 | GQ452347 |
| *Murdannia* | AY298838 | KP083044 |
| *Najas guadalupensis* | KM502156 | KM501964 |
| *Najas sp C113* | DQ859170 | KF632809 |
| *Narthecium* | AJ286560 | AB040162 |
| *Nechamandra alternifolia* | U80706 | AB506767 |
| *Nypa* | M81813 | AM114552 |
| *Orontium aquaticum* | AJ005632 | AM920550 |
| *Oryza* | D00207 | AF148650 |

(continued)

**Table 5.5** (continued)

| Taxon | rbcL | matK |
|---|---|---|
| *Ottelia ovalifolia* | DQ859171 | KF632811 |
| *Petrosavia* | AF206784 | AB040161 |
| *Philesia* | Z77302 | AY624479 |
| *Philydrum* | AY299824 | AY299824 |
| *Phyllospadix iwatensis* | na | AB096172 |
| *Phyllospadix japonicus* | JQ995760 | JQ990932 |
| *Phyllospadix scouleri* | DQ859172 | KF632812 |
| *Phyllospadix torreyi* | U80731 | JQ990934 |
| *Pleea tenuifolia* | AJ131774 | AF465301 |
| *Posidonia australis* | HQ901573 | KF488514 |
| *Posidonia oceanica* | U80719 | GQ927729 |
| *Potamogeton lucens* | HM850280 | JF955620 |
| *Potamogeton natans* | AB196946 | KF632814 |
| *Puya* | L19973 | EU780853 |
| *Ranalisma* | JF781051 | KF632823 |
| *Ruppia cirrhosa* | JQ034322 | KC505607 |
| *Ruppia megacarpa* | JQ034324 | KC505609 |
| *Ruppia polycarpa* | AB507898 | AB507938 |
| *Ruppia tuberosa* | AB507899 | AB507939 |
| *Sagittaria* | L08767 | HQ456468 |
| *Sarcandra* | AY236833 | AJ966796 |
| *Scheuchzeria palustris* | U03728 | KJ939690 |
| *Schisandra* | L12665 | AY326509 |
| *Smilax* | Z77310 | AB040204 |
| *Stemona* | AJ131948 | AB040210 |
| *Stratiotes aloides* | HQ901565 | AB002576 |
| *Symplocarpus foetidus* | FJ875025 | AM920551 |
| *Syringodium filiforme* | KF488496 | KF488511 |
| *Syringodium isoetifolium* | KF488497 | KF488512 |
| *Tacca chantieri* | AJ235810 | KP083036 |
| *Talbotia elegans* | AY149358 | AY491664 |
| *Tamus communis* | AF307474 | AJ581408 |
| *Tasmannia lanceolata* | AY298851 | KP407454 |
| *Thalassia hemprichii* | AB002577 | AB004897 |
| *Thalassia testudinum* | HQ901568 | na |
| *Thalassodendron ciliatum* | KF488513 | KF488498 |
| *Thalassodendron pachyrhizum* | U80692 | na |
| *Tofieldia* | AJ286562 | AM920648 |
| *Triglochin maritima* | HQ901578 | AB088782 |
| *Triglochin palustris* | DQ859176 | GQ452340 |

(continued)

**Table 5.5** (continued)

| Taxon | rbcL | matK |
|---|---|---|
| *Trillium* | D28164 | AB07392 |
| *Typha* | M91634 | KP083057 |
| *Vallisneria americana* | U03726 | AY957575 (*V. asiatica*) |
| *Veratrum* | D28168 | AB017417 |
| *Zannichellia palustris* | HQ901572 | JN034096 |
| *Zostera marina* | AB906846 | JN034097 |

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# Chapter 6
# Genetic Connectivity in Tropical and Temperate Australian Seagrass Species

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**Abstract** Connectivity among populations influences resilience, genetic diversity, adaptation and speciation, so understanding this process is fundamental for conservation and management. This chapter summarises the main mechanisms of gene flow within and among seagrass meadows, and what we know about the spatial patterns of gene flow around Australia's coastline. Today a significant body of research on the

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demographic and genetic connectivity of Australian seagrass meadows has developed. Most studies have focused on the genera *Posidonia*, *Zostera*, *Heterozostera* and *Thalassia*, in tropical and temperate systems across a range of habitats. These studies have shown overwhelmingly, that sexual reproduction is important for meadow persistence, as in most cases Australian seagrass meadows are genotypically diverse, with moderate to high levels of genotypic diversity. This high diversity could be generated through demographic connectivity, recruitment of individuals sourced from within a meadow, or from dispersal between meadows. Attempts to understand the relative significance of these processes are limited, highlighting a major gap in our understanding. Genetic structure is apparent across a range of spatial scales, from m's to 100's to 1000's km. At local and regional scales, particularly in confined systems such as estuaries and bays, it is not necessarily the dominant oceanographic currents influencing patterns of genetic connectivity, but local eddies, winds and tides. Over larger spatial scales, isolation by distance is consistently significant, with unique genetic clusters spreading over 100s of kilometres. This indicates that regional structure occurs at the limits of long distance dispersal for the species and this is particularly evident where meadows are highly fragmented. The number of genetic studies on Australian seagrasses has increased dramatically recently; however, there are still many opportunities to improve our understanding through focusing on species with different dispersal potentials, more detailed sampling across a range of spatial and temporal scales and combining ecological and modelling approaches.

## 6.1 Introduction

Connectivity among populations influences resilience, genetic diversity, adaptation and speciation, so understanding this process is fundamental for conservation and management (Ellstrand 2014). Australia is a unique region for seagrass scientists due to the high diversity of seagrass species and among these, the full range of life history and morphological traits that are found in seagrasses globally (Kilminster et al. 2015). Most species have broad distributions (Short et al. 2007), but are not continuously distributed, forming populations of varying sizes and potentially different levels of connection. In addition, Australia spans temperate and tropical climate zones, and as such, seagrasses grow in a variety of habitats with different environmental drivers that can influence population genetic connectivity (Kilminster et al. 2015). This chapter synthesizes our current understanding of population genetic connectivity in Australian seagrasses. The aims of this chapter are to:

- summarise the main mechanisms of gene flow that lead to genetic connectivity among seagrass meadows and how it is measured;
- summarise the patterns of gene flow in relation to the spatial scale and environmental drivers of genetic connectivity; and
- identify existing knowledge gaps in our understanding of genetic connectivity.

Genetic connectivity or gene flow can be defined as the proportion of newly immigrant genes moving into a given population (sensu Endler 1977) or, alternatively, *N*m, the absolute number of individuals exchanged between populations per generation (Wright 1951). This is different to demographic connectivity, which is a measure of the relative contributions of dispersal versus local recruitment to population growth (Waples and Gaggiotti 2006; Lowe and Allendorf 2010). Kendrick et al. (2017) propose a framework for integrating both demographic and genetic connectivity where genetic connectivity is separated into contemporary connectivity from recent successful dispersal of pollen and seeds or historical connectivity, the result of successful dispersal events over multiple generations. This chapter will, where possible, examine both gene flow among populations and local recruitment patterns within populations inferred from genetic methods.

In many plant species, most of the seeds will not disperse far, remaining within the population they originated in (Nathan 2006). Thus, they will contribute to demographic connectivity and maintenance of the local population through the addition of new recruits. If the seeds are dormant and a seedbank develops, this provides a mechanism for ongoing local recruitment through time. A seedbank also provides resilience to the meadow, allowing recovery following disturbance (Unsworth et al. 2015). Dispersal beyond the original meadows by seeds that eventually recruit may establish new populations and/or facilitate genetic connectivity evidenced by gene flow. Although most seeds remain close to the parent, long distance dispersal does occur, although it is rare (Nathan 2006). In marine systems, because many species may have large mean dispersal distances, dispersal at regional scales may drive local dynamics (Kinlan and Gaines 2003).

Understanding the spatial and temporal scales of genetic connectivity provides insights into population biology and evolution. From an evolutionary perspective, barriers to gene flow can facilitate speciation and we see this with the land barrier between the Indo-Pacific and Atlantic Oceans, or the Red Sea and the Mediterranean, where distinct species assemblages are found (Short et al. 2007). The disruption of the land barrier between these oceans by the opening of the Suez Canal has led to the introduction of *Halophila stipulacea* to the Mediterranean where it is now well established (Lipkin 1975). Genetic connectivity data can provide insights into both historical population isolation (Alberto et al. 2008), as well as more contemporary connectivity processes (Serra et al. 2010). It can also be used to inform restoration and conservation actions (Evans et al. 2014), including the identification of genetically depauperate populations, isolated populations and the significance of sexual reproduction, all of which inform on the resilience of populations to withstand or recover from disturbance (refer to Chap. 20: Decline and Restoration Ecology of Australian Seagrasses).

The level of gene flow among populations is primarily dependent on interactions between the mode of reproduction, the mobility of individuals and their propagules (Lowe et al. 2004), and local hydrodynamic flows. However, dispersal facilitated by animals or through human activities such as shipping, can also contribute to gene flow (e.g. Serra et al. 2010; Coyer et al. 2013; McMahon et al. 2014). Seagrasses have a variety of reproductive strategies due in part, to the polyphyletic nature of the group across four independent lineages (Les et al. 1997) and the various adaptations for underwater sexual reproduction and dispersal. These strategies include, clonal and sexual reproduction with a number of sexual reproductive modes, including hermaphrodism (male and female flowers on the same individual, within the same structure), monoecy (male and female flowers on the same individual) and dioecy (male and female flowers on different individuals) (refer to Chap. 8: Reproductive, Dispersal and Recruitment Strategies in Australian Seagrasses). They also have a number of different strategies for the dispersal of pollen, fruits and other propagules such as viviparous seedlings (Kendrick et al. 2012). Therefore, the magnitude of genetic connectivity is likely to vary among species due to these different reproductive modes and mating strategies. The magnitude of genetic connectivity is also likely to vary across the distributional range of a species as the historical and contemporary environmental processes, which also influence gene flow vary in space.

The dispersal of pollen, fertilisation and production of sexually produced propagules, as well as the movement and recruitment of fruits and seeds is extremely difficult to monitor in situ. Successful recruitment or gene flow can be estimated by the use of molecular markers and calculating microevolutionary processes evidenced through changes in allele frequencies through a population genetic approach. There are a plethora of population genetic markers available but microsatellite DNA markers are the most commonly used to date in seagrass studies, providing adequate resolution to examine genetic and demographic connectivity processes. Microsatellite markers are generally regarded as neutral, i.e. the loci are not under selection, and hence meet the assumptions of many of the population genetic analyses. The recent and ongoing development of microsatellite DNA markers for many Australian seagrass species will improve our understanding of genetic connectivity processes in marine plants: *Posidonia australis* (Sinclair et al. 2009); *Zostera muelleri* (Sherman et al. 2012); *Heterozostera nigricaulis* (Smith et al. 2013) (for the current status of the genus *Heterozostera*, see Appendix); *Cymodocea rotundata* (Arriesgado et al. 2014b); *Cymodocea serrulata* (Arriesgado et al. 2014a); *Thalassia hemprichii* (Wainwright et al. 2013b; van Dijk et al. 2014); *Halophila ovalis* (Xu et al. 2010); *Enhalus acoroides* (Nakajima et al. 2012), *Syringodium isoetifolium* (Matsuki et al. 2013; Wainwright et al. 2013a), *Halodule uninervis*, *Ruppia tuberosa* and *Amphibolis antarctica* (van Dijk personal communication).

Emerging techniques for population genetic analysis include genotype by sequencing approaches incorporating single nucleotide polymorphisms (SNPs, Oetjen et al. 2010). SNP's are generated through next generation sequencing techniques and 100s to 10,000s of loci are commonly detected (Fischer et al. 2017). SNP's are not necessarily neutral, so adaptation to different environmental conditions can also be investigated. SNP's are usually biallelic and generally have a lower information content than microsatellite markers per locus, so a greater number are required to assess the patterns of genetic diversity and population connectivity (Van Inghelandt et al. 2010; Fischer et al. 2017). Recent comparisons of both marker types in breeding stock suggest that approximately 2–3 SNPs are needed per microsatellite locus to obtain similar resolution (Gärke et al. 2012; Fernandez et al. 2013). The much larger number of markers obtained during SNP discovery suggests they will provide better resolution to assess demographic connectivity, which is often challenging in marine systems and with potentially long-lived clonal plants (Corander et al. 2013; Gagnaire et al. 2015; Fischer et al. 2017). In addition, they generate information (e.g. haplotypes), which could be useful for deducing historical relationships and processes and enable identification of cryptic taxa and hybridization events (Ogden et al. 2013; Larson et al. 2014).

## 6.2 Mechanisms of Genetic Connectivity

Four life-history stages of seagrasses contribute to realised levels of gene flow: pollen, sexually produced propagules (including non-buoyant and buoyant seeds and fruits, viviparous seedlings, specialized shoots e.g. spathes, cymes or rhipidia), vegetative fragments and through the process of clonal growth by long-lived clones (McMahon et al. 2014). Pollen-mediated gene flow generally occurs at the scale of a meadow and is achieved when pollen reaches a receptive female flower and fertilises it. Sexually produced propagules are the main mechanism that seagrasses disperse and connect to other meadows. The forms of reproductive propagules vary greatly across species, from buoyant fruits to non-buoyant dormant seeds. Dispersal of sexually derived propagules has a greater potential to influence the levels of genetic connectivity among populations compared to pollen-mediated gene flow, due to the potential for greater dispersal distances. Genetic connectivity is also realised via dispersal of reproductive propagules by biotic vectors, such as birds, fish or turtles (Kendrick et al. 2012). Vegetative fragments may also contribute to and influence genetic connectivity, however, the main difference to sexually-produced propagules is that they have the same genetic make-up as the parent plant, and thus do not contribute new genetic material or recombination into local populations. However, dispersal of vegetative fragments and subsequent recruitment beyond their local meadow will result in gene flow among populations. Our current understanding of how these different mechanisms contribute to genetic connectivity is described below.

### *6.2.1 Pollen-Mediated Gene Flow*

Pollen-mediated gene flow is defined as the movement of pollen from the anther of a male flower to fertilise the ovary of a female flower resulting in seed set and the development of sexually derived propagules (Ducker et al. 1978). Seagrass pollen in water-pollinated species is unusual in possessing one of two forms; (1) flexible filiforme shape (lacking an exine) or (2) being formed into long, filamentous aggregations of pollen grains (Ackerman 1995). Both types of pollen result in the formation of large dispersal units having neutral buoyancy. Water flow and currents serve as the main vector for pollen dispersal and capture in seagrasses (Ackerman 1997a; Verduin et al. 2002). Pollen is transported in three main ways; (1) above, (2) on, and/or (3) beneath the water surface with many seagrass species often utilizing a combination of two or more methods (Cox et al. 1992a) (Table 6.1). Submarine pollination has been observed in several seagrasses including *Zostera marina* (Ackerman 1997b), *Thalassia testudinum* (Cox and Tomlinson 1988),

**Table 6.1** Summary of characteristics for sexual reproductive traits in Australian seagrass genera

| Genera | Reproductive system[a] | Pollen movement[a] | Sexual propagule[a] | Buoyancy[b] | Seed bank dormancy[b] |
|---|---|---|---|---|---|
| **Hydrocharitaceae** | | | | | |
| *Enhalus* | Dioecious | Surface | Fruit, seed | Good | No dormancy |
| *Thalassia* | Dioecious | Submarine | Fruit, seed | Good | No dormancy |
| *Halophila* | Dioecious and monoecious | Surface and submarine | Fruit, seed | Moderate/ poor | Transient/ persistent |
| **Cymodoceacae** | | | | | |
| *Amphibolis* | Dioecious | Submarine | Seedling | Good | Viviparous |
| *Cymodocea* | Dioecious | Submarine | Fruit | Poor | Persistent |
| *Halodule* | Dioecious | Submarine | Fruit | Poor | Persistent |
| *Syringodium* | Dioecious | Submarine | Fruit | Poor | Persistent |
| *Thalassodendron* | Dioecious | Submarine | Seedling | Good | Viviparous |
| **Posidoniaceae** | | | | | |
| *Posidonia* | Monoecious and hermaphroditic | Submarine | Inflorescence, fruit, seed | Good | No dormancy |
| **Zosteraceae** | | | | | |
| *Phyllospadix* | Dioecious | Surface and submarine | Rhipidia, spathe, seed | Moderate | Transient |
| *Zostera* and *Heterozostera* | Monoecious | Surface and submarine | Rhipidia, spathe, seed | Good/ moderate | Transient |
| **Ruppiaceae** | | | | | |
| *Ruppia* | Monoecious | Surface and submarine[c] | Seed[c] | Poor[e] | Persistent[e] |
| **Potamogetonaceae** | | | | | |
| *Lepilaena* | Monoecious | Submarine[d] | Fruit[d] | Poor[d] | Persistent[f] |

Seed bank dormancy: indistinct refers to the lack of a dormancy period; viviparous as seedlings that develop on mother plant; transient as seeds that are dormant but turnover in <1 year; and persistent, seeds that are dormant but remain viable for >1 year. Subscripts refer to references from which this information is sourced

[a] Ackerman (2006)
[b] Orth et al. (2006)
[c] Jacobs and Brock (2011)
[d] Jacobs and McColl (2011)
[e] Ailstock et al. (2010)
[f] Porter et al. (2007)

**Fig. 6.1** Pollen dispersal in the *Halophila ovalis* along the water surface at low tide, Pioneer Bay, Airlie Beach, Queensland. Photographs by Kor-Jent van Dijk

*Phyllospadix scouleri* (Cox et al. 1992b), *Amphibolis antarctica* (Verduin et al. 1996) and *Posidonia australis* (McConchie and Knox 1989). Pollination occurs on the water surface in *E. acoroides* (Kendrick et al. 2012) and *H. ovalis* has been observed to release pollen on the water surface at low tide (Cox and Knox 1989) (Fig. 6.1). Most studies, either through direct measurements and modelling or genetic inference have demonstrated pollen dispersal over distances up to 15 m (McConchie and Knox 1989). However, recent work by Sinclair et al. (2014a) using paternity assignment procedures estimated average distances of 30 m up to a maximum of 178 m in *P. australis*. *Posidonia australis* is the only Australian seagrass species where pollen-mediated gene flow has been examined using genetic markers while detailed physical and reproductive ecology has been examined in *A. antarctica*. These field observations, model simulations and molecular studies demonstrate the effectiveness of water to move and mix pollen within the marine environment. A new phenomenon, zoobenthophily or the facilitation of pollen transfer by marine invertebrates, has recently been described in the tropical Atlantic seagrass *Thalassia testudinum* (van Tussenbroek et al. 2012). Mesocosm experiments showed that fertilisation rates did not decline with distance (up to 150 m) between male and female flowers in the presence of marine invertebrates, thus the fauna were likely extending the dispersal range of pollen (van Tussenbroek et al. 2016). This mechanism has not been recorded in Australian species.

### 6.2.2 Sexually Produced Propagule Mediated Gene Flow

Seagrasses form a wide variety of sexual propagules including seeds, fruits, rhipidia and viviparous seedlings (Table 6.1 and Fig. 6.2). These sexually produced propagules are released from the parent plant as positively buoyant (e.g. *Thalassia* and *Posidonia* fruits), neutrally buoyant (e.g. viviparous *Amphibolis* seedlings) or negatively buoyant propagules (e.g. *Halophila* or *Halodule* seeds) (Fig. 6.2). Water movement driven by currents, waves, tides and wind will affect the dispersal distance of positively and neutrally buoyant structures, whereas sediment movement will affect the movement of negatively buoyant propagules. The dispersal potential of a sexually produced propagule is dependent on the duration of these different reproductive stages such as how long the fruit is buoyant for and how long seeds remain viable (Kendrick et al. 2012). Species with a buoyant phase have a higher potential to disperse greater distances.

Recent studies indicate marine connectivity cannot be simplified as predominately an isolation-by-distance model (White et al. 2010; Kendrick et al. 2012; Ruiz-Montoya et al. 2015). These studies suggest the frequency of connectivity will be strongly influenced by environmental factors such as oceanic currents, depth profiles, changing water flows and gyres. As a result, a model has been proposed where the timing of seagrass propagule release is an important trait that has evolved under selection for dispersal and recruitment success (McMahon et al. 2014). Following the dispersal phase, settled seeds will generally remain in the local area they settled in but significant secondary movement can occur if turbulence is high

**Fig. 6.2** Pictures of sexually produced propagules. *Thalassodendron pachyrhizum* (KM). *Amphibolis griffithii* (KM). *Posidonia coriaceae* (MW). *Halodule uninervis* seed bank (MW). *Halophila ovalis* floating fragment with fruit (AR). Photographs courtesy of Kathryn McMahon (KM), Michelle Waycott (MW) and Angela Rossen (AR)

enough or mass sediment transport occurs (Kendrick et al. 2012). Ingestion by herbivores can also be an important means of long distance dispersal. Hard-coated seeds that travel through the digestive system undamaged have the potential for long distance dispersal; this is discussed below.

There are a number of direct and indirect ways to assess genetic connectivity, and all are based on a number of assumptions and models of marker inheritance (Lowe and Allendorf 2010; Kendrick et al. 2017). In seagrasses, and other clonal organisms, it is important to evaluate the genotypic diversity within a meadow as this will provide insight into the overall size of the population (based on the number of clones present), as well as indicate the relative importance of sexual reproduction (Reusch 2001). High genotypic diversity indicates that sexual reproduction is important for maintaining populations, conversely, low genotypic diversity where a few genotypes dominate (e.g. Evans et al. 2014) indicates that population maintenance relies on asexual reproduction, most likely through vegetative expansion of the few individuals that establish in the population.

The two most commonly applied population genetic measures to date, on Australian seagrasses, from which genetic connectivity can be inferred indirectly are $F_{ST}$ and Isolation by Distance (IBD). The first measure, and the most widely used, $F_{ST}$, is a measure of genetic differentiation, ranging between 0 and 1, where lower values indicate less genetic differentiation and therefore greater connectivity (Wright 1943, 1951). This measure is dependent on the type of markers used so comparing $F_{ST}$ values among studies using different markers and between species has some limitations, although analytical methods have been developed to improve the ability for such comparisons to be effective (Meirmans and Hedrick 2011; Verity and Nichols 2014). Under a number of assumptions the number of immigrants can be estimated from $F_{ST,}$ leading to indirect estimates of genetic connectivity.

The second measure commonly used as an indirect measure of connectivity, Isolation by Distance (IBD) (Wright 1943), examines the relationship between spatial distance and genetic distance among individuals or populations. It refers to the accrual of local genetic variation under geographically limited dispersal (Holsinger and Weir 2009; Meirmans and Hedrick 2011). A significant IBD relationship is often used to infer that populations closer together are more likely to undergo genetic exchange. Thus, the spatial scale over which there is a significant relationship between geographic distance and genetic differentiation provides a measure of the scale over which gene flow occurs.

More direct measures of genetic connectivity such as paternity analysis, population assignment or the modelling of migration rates generally have fewer assumptions, but require more data and have not been used as consistently in Australian seagrass studies. Some of these methods identify directional migration of immigrants between populations using either Bayesian assignment methods such as BAYESASS (Wilson and Rannala 2003) or other modelling approaches. They do not necessarily estimate migration directly, but cluster panmictic sites and distinguish regions of discontinuity under a range of modelled scenarios as has been implemented for example in the software package STRUCTURE (Pritchard et al. 2000; Evanno et al. 2005). Estimating these discontinuities without making a priori assumptions as to the number and sizes of populations among discontinuously sampled systems can be useful in identifying breaks in genetic connectivity leading to more biologically realistic estimates of gene flow. A range of other techniques are available and evolving to estimate connectivity (summarised in Kendrick et al. 2017), but to date have rarely been applied in Australian seagrass data sets.

Finally, direct measures of dispersal can occur for some species through the release and tracking of dispersing propagules themselves under a range of situations as has been achieved for the buoyant fruits of *Thalassia* and *Posidonia* (van Dijk et al. 2009; Ruiz-Montoya et al. 2015). Modelling of fruit dispersal by combining hydrodynamic and particle transport models which incorporate the physical properties of fruits and seeds that influence dispersal such as buoyancy, timing of release and duration of viability, is another approach to understanding potential contemporary genetic connectivity in seagrasses (Grech et al. 2016; Sinclair et al. 2016b; Hernawan et al. 2017).

### *6.2.3 Dispersal of Vegetative Fragments*

Vegetative fragmentation of seagrass can result from physical disturbances (e.g. storms or grazing) and successful dispersal can primarily occur from three forms, (1) “ramet fragments” which are segments of adult plants including rhizomes and shoots, that have been dislodged and broken off from the main plant (Balestri et al. 2011); (2) “clonal propagules” which are asexually produced, recruitment viable parts of a seagrass plant (Kuo et al. 1987; Thomson et al. 2015)[1]; (3) “pseudoviviparous plantlets” where whole miniature plants are produced in the reproductive structures (Ballesteros et al. 2005; Sinclair et al. 2016a). The dispersal modes will vary in effectiveness for these alternative vegetative units. Ramet fragments and clonal propagules may be dispersed by water currents to another location and, as a unit capable of independent life, they may settle and establish in new available habitats allowing the seagrass to expand the population (Di Carlo et al. 2005). The successful establishment of vegetative fragments appears to be dependent on the stability of the substrate, with greater stability showing greater survival (Campbell 2003; Di Carlo et al. 2005). Dispersal and successful recruitment of vegetative fragments has been observed in *Heterozostera* (Coyer et al. 2013) and *Posidonia* (Campbell 2003). The prolonged buoyancy and viability of vegetative fragments indicate a strong dispersal potential in *Heterozostera* (Stafford-Bell et al. 2015; Thomson et al. 2015) with several documented examples of long distance dispersal events (Coyer et al. 2013; Sherman et al. 2016; Smith et al. 2018). Prolonged buoyancy, viability and successful establishment (30% of fragments) has also been documented in *Thalassia*, suggesting this as a potential

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[1] Note Thomson et al. (2015) define these as viviparous propagules, but this term is incorrect. Viviparous propagules are sexually produced propagules that develop on the mother plant. We use the term asexually or clonally derived propagules in this case.

mechanism for long distance dispersal (Wu et al. 2016). There are no data of how long pseudoviviparous plantlets remain buoyant and whether they can recruit, however, the lack of observations of plantlets in the surrounding *P. australis* meadow suggests that longer distance dispersal may be possible (Sinclair et al. 2016a) although this is only speculation. Despite their well recognised existence, seagrass vegetative fragments ability to recruit following dispersal is a poorly understood biological process (McMahon et al. 2014).

Genetic identification of individual plants (i.e. genets or multilocus genotypes—MLG's) is required to determine if vegetative propagules have dispersed, and this requires genetic markers of an appropriate resolution to detect genets with high probability (Arnaud-Haond et al. 2005). Once marker systems are available, it is still a challenge to assess the importance of vegetative propagules as a mechanism for dispersal between populations. This is due to the number of fragments produced coupled with the extremely rare nature of successful recruitment resulting in an extremely low probability that shared MLG's that have arisen from dispersal and recruitment of clonal propagules will be detected. However, when the frequency and scale of clonal fragments and recruitment are adequate, they can be detected, for example 3.5–9% of samples genotyped in the Mediterranean seagrass *Posidonia oceanica* were shared among meadows (Arnaud-Haond et al. 2012). Detection will be easier in populations with only a few abundant genotypes, but harder for species with high rates of recruitment through sexual reproduction and high genotypic diversity, requiring intensive sampling to capture most of the genotypes within a meadow. The relationship between sample number and number of genotypes will be auto-correlated with the typical dispersal distance within populations. Thus a landscape style approach to sampling in which samples are collected at regular intervals may prove to be a better option, rather than the more traditional clumped, population sampling methods (Bricker et al. 2011).

The genetic identification of samples with the same genotype within meadows—can be due to two processes: (1) clonal growth spreading the individual over space with time followed by natural or disturbance induced fragmentation, or (2) fragmentation involving the dispersal of the clonal propagules via water followed by settlement and recruitment. It is not clear how to separate this under natural conditions. More work is needed to determine the frequency of fragmentation of viable ramets, the longevity of viable fragments and the success of establishment. Hydrodynamics combined with particle transport modelling could incorporating these biological conditions could provide predictions of the probability of this mode of dispersal.

### 6.2.4 *Biotic Dispersal*

Biotic-mediated dispersal is an emerging field of research in seagrasses. There are a variety of potential biotic vectors that feed on, or live in, seagrass habitat including dugongs, manatees, turtles, waterfowl, fish and invertebrates (McMahon et al. 2014).

Pollen, sexual propagules and vegetative fragments can be dispersed attached to animals, or seeds can be ingested and then deposited through defecation. Biotic dispersal has been measured over distances of meters up to 1000 km. For example movement of *Thalassia* pollen by marine invertebrates has been observed, with potential dispersal over meters (van Tussenbroek et al. 2012, 2016). Birds can move vegetative fragments and seeds of *Ruppia*, *Zostera* and *Halophila* over hundreds of kilometres and potentially across continents (Figuerola et al. 2002; Charalambidou et al. 2003; Isada and Bermejo 2009; Wu et al. 2016) and *Zostera* and *Halophila* seeds can be dispersed by fish (200 m) or turtles (up to 1.5 km) (Sumoski and Orth 2012; Tulipani and Lipcius 2014; Wu et al. 2016). There are a number of traits in seagrasses that are likely to be important for successful biotic dispersal, either through attachment to vectors or through ingestion. The viability time of the pollen, reproductive propagule and/or vegetative fragment is critical when seagrass material is attached to adult plants, and for seeds that are ingested, only those with a hard seed coat are likely to survive passage through the digestive tract of an animal vector.

In the Australian context, there is emerging evidence for dispersal following consumption by dugongs (*Dugong dugon*) as seeds are present and viable in dugong faeces. Seeds from a number of tropical seagrass species have been found in dugong faeces, *Halophila ovalis*, *H. decipiens, Halophila* sp., *Zostera muelleri* and *Halodule uninervis*, all of which have been reported as either intact or viable after passing through the dugong digestive tract (Table 6.2). The occurrence of seeds in dugong faeces is relatively low, 5% of faeces samples collected have had

**Table 6.2** A summary of the type and amount of seeds found in dugong faeces and the viability these seeds

| Location | Proportion of dugong faeces containing seeds | Species | Viability | Reference |
|---|---|---|---|---|
| Moreton Bay, Qld | 5% (n = 42) | *H. ovalis* | 1/3 germinated | McMahon (unpublished data) |
| Hervey Bay, Pioneer Bay, Rods Bay, Lagoon and Shelley Beach, Qld | 19% (n = 21) | *Z. muelleri*<br>*H. uninervis* | 43% viability[a]<br>37% unviable<br>20% partly digested | Waycott (unpublished data) |
|  | Number seeds per g DW dugong faecal matter |  |  |  |
| Qld | 2.6 | *Z. muelleri*<br>*H. uninervis*<br>*H. decipiens*<br>*Halophila* sp. | 9.1% viable[b] | Tol et al. (2015) |

[a] Determined viable if embryo intact
[b] Determined viable with stain

seeds present (McMahon and Waycott, unpublished data) (Tol et al. 2015), and which were collected at a time when seeds were present in the sampling locations. Tol et al. (2015) found on average 2.62 ± 0.56 seeds per gram dry dugong faecal matter and on average 9.1 ± 4.6% of seeds were viable. Further work is required to understand the probability of survival of these seeds following germination.

Genetic data can be used to infer the role of biotic vectors in dispersing seagrass propagules within and between meadows and with long distance dispersal by assessing the congruence between genetic connectivity patterns and the biotic vector movement patterns (Triest and Sierens 2013), although these studies are very limited. Population genetic data has been collected for *H. ovalis* in Moreton Bay, however, there was no strong evidence for dugongs dispersing seeds between meadows over distances of 1–15 km (McMahon 2005).

## 6.3 Patterns of Genetic Connectivity in Australian Seagrasses

A significant body of research on the demographic and genetic connectivity of Australian seagrass meadows (Fig. 6.4) has developed and the majority is presented in the individual case-studies in the next section. These studies have shown overwhelmingly, that in most cases, Australian seagrass species are genotypically diverse, with moderate to high genotypic diversity. However, almost all studies have identified one or two meadows with low genotypic diversity, and this has been observed consistently towards range edges; northern range edge for *Z. muelleri* in tropical Queensland (van Dijk, unpublished data), the northern range edge for *P. australis* on the east coast of Australia (Evans et al. 2014) and the southern range edge of *T. hemprichii* on the east coast of Australia (van Dijk, unpublished data). These highly clonal meadows are dominated by a few genotypes and indicate two key points: firstly, these populations are persisting in the absence of, or with only very low sexual reproduction; secondly, that genetic connectivity towards these edge of range populations must be low. It remains untested as to the cause of the low diversity. Is it the result of selection for genotypes adapted to the edge of range environmental conditions? Or, is it the result of very rare long distance dispersal or a very low frequency of recruitment coupled with rare dispersal?

The majority of genetic connectivity studies to date have worked within local scales of 100 km, such as in lakes (Sherman et al. 2016), embayments (Sinclair et al. 2014b; Jenkins et al. 2015) or island groups (Hernawan 2016). There is significant genetic structure across a range of spatial scales, within a meadow, between sites in a location and among locations. Isolation by distance (IBD) is not always significant, an increasing distance between sites, does not necessarily mean greater genetic differentiation, and less genetic connectivity. At these local and regional scales in these more confined systems, it is not the dominant oceanographic currents influencing patterns of genetic connectivity, but local eddies, winds and tides. Interestingly, a range of authors (Sinclair et al. 2014b; Jenkins et al. 2015; Sherman et al. 2016) did find isolation by distance over a small scale (~16 km), but this did not hold when tested across the larger scales (~45 km). This loss of the IBD relationship was described as being the result of complex seascape features and specific hydrodynamic conditions in the area. However, even over regional scales, barriers to gene flow are sometimes detected, as demonstrated by Hernawan (2016), which are explained by local currents influencing dispersal and habitat effects most likely acting on recruitment and survival.

At the larger scale, over 600–1500 km isolation by distance is significant, and significantly different genetic clusters form, spreading over 100s of km (Sinclair et al. 2016b, van Dijk, unpublished data). There appears to be lower levels of genetic connectivity among spatially fragmented populations along the east coast of Australia. In temperate, estuarine species, the relative isolation of different estuaries may act as a barrier to dispersal. For example, during periods of higher sea levels, St Georges Basin, south of Sydney, would have formed an open embayment. However, the basin remains largely enclosed with only a narrow 6.5 km opening to the ocean, thus in reality, the probability of seed dispersal is very low and this meadow is significantly genetically differentiated from neighbouring meadows (Evans et al. 2014). Connectivity could be limited by the ecological or biological limits of a species, such as the maximum dispersal distances being less than the next suitable habitat. Kendrick et al. (2012) suggested this was 400 km, and the studies emerging from Australia support this, that is, significant regional structure occurs at the limits of LDD for the species and this is particularly evident where meadows are highly fragmented. Thus, connectivity and the processes acting locally within a region are far more important to seagrasses than the large offshore boundary currents. Of course, there are occasional exceptions to this rule, such as the long-distance dispersal of *H. nigricaulis (chilensis)* (Coyer et al. 2013; Smith et al. 2018).

## 6.4 Case-Studies of Genetic Connectivity

Here we present case studies on the genetic connectivity of five common Australian seagrass genera, *Posidonia* (*P. australis*), *Zostera* (*Z. muelleri*) and *Heterozostera* (*H. nigricaulis*, grouped into *Zosteraceae*), *Halophila* (*H. ovalis*) and *Thalassia* (*T. hemprichii*). These genera were selected as they represent the three main seagrass lineages (*Hydrocharitaceae*, *Cymodoceacea* and *Zosteraceae*), have a range of biological traits that potentially influence dispersal and genetic connectivity (e.g. buoyant vs. non-buoyant seeds), and most of the published literature is based on them. The examples provided cover both tropical and temperate environments, represent all seagrass biogeographic zones in Australia, most Australian states and a range of habitats including estuaries, protected and exposed coastal areas, as well as intertidal and subtidal meadows. Eastern and south-eastern Australia are the best covered regions, with the isolated and very remote north and north-west part of Australia poorly represented (Fig. 6.4).

### 6.4.1 *Case Study* Posidonia australis

*Posidonia australis* is the most widespread of the eight currently recognised temperate Australian *Posidonia* species, forming dense single or mixed species meadows in shallow, subtidal estuarine and coastal habitats (Cambridge and Kuo 1979). It is distributed from Shark Bay, WA around to Wallis Lake, NSW, including northern Tasmania (Waycott et al. 2014). The flowers are hermaphroditic or bisexual, each containing a single ovule (Remizowa et al. 2012) and form in groups on specialized shoots (Fig. 6.3). Buoyant fruits are produced which can disperse over a 100 km. Three regional genetic connectivity studies have been

**Fig. 6.3** *Posidonia australis* reproductive and dispersal phases. Left: Flower emerging from meadow. Right top: Pollen release. Right middle: Reproductive shoot with fruits developing. Right bottom: Aggregation of buoyant fruits. Photographs courtesy of Angela Rossen

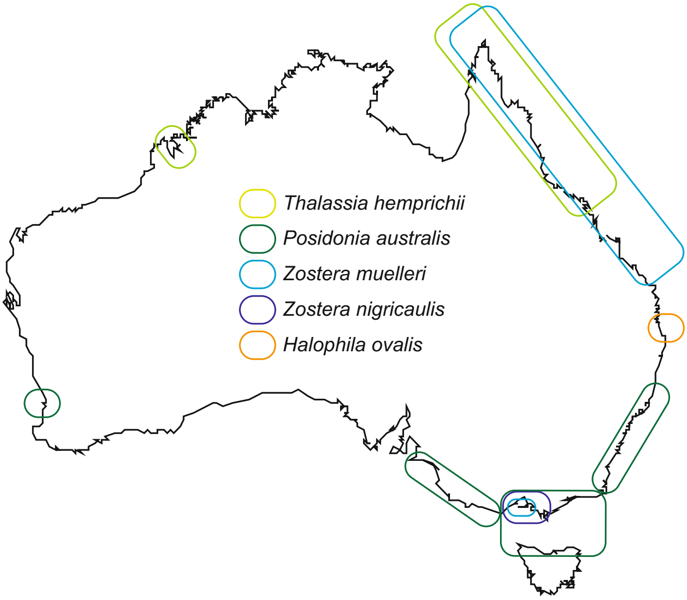

**Fig. 6.4** Location and focal species for seagrass genetic connectivity studies in Australia

published so far (Evans et al. 2014; Sinclair et al. 2014b, 2016b) (Fig. 6.4), although the entire species range has not been completed. Two of these regional studies have been interpreted with the aid of regional hydrodynamic models (Ruiz-Montoya et al. 2015; Sinclair et al. 2016b).

#### 6.4.1.1 Pollen-Mediated Gene Flow

Floral development in the bisexual *P. australis* is initiated during April–May (Austral autumn), as water temperatures fall and day length shortens (McComb et al. 1981). Large quantities of 'sticky' pollen are released from the anthers of flowers held on long inflorescences over a 6-week period through August and September and individual pollen grains remain suspended in the water and have been shown to be viable for up to 50 h after release (Smith and Walker 2002) (Fig. 6.3). The extended period of pollen release in *P. australis* overlaps with other *Posidonia* species (Smith and Walker 2002), providing an opportunity for hybridization among locally sympatric species.

High rates of outcrossing obtained in a mating system study conducted in two *P. australis* meadows in Perth metropolitan waters (Table 6.3) (Sinclair et al. 2016a) are consistent with a completely outcrossed species. Average pollen dispersal distances inferred from paternity assignment (26.8–30.8 m) were larger than the mean clone size (12.8 and 13.8 m). This suggests that pollen is able to disperse beyond the source clone or that the probability that the pollen finds a stigma of the

**Table 6.3** Pollen-mediated gene flow measures for Australian seagrasses

| Species | Outcrossing rates | Dispersal distances Avg (Max) | Reference |
|---|---|---|---|
| **Posidoniaceae** | | | |
| *P. australis* | 0.10–0.89[a] | | Waycott and Sampson (1997) |
| *P. australis* | 0.98–1.0[b] | 30 (178 m) | Sinclair et al. (2014a) |
| *P. australis* | | 30 (120 m) | Smith and Walker (2002) |
| *P. sinuosa* | | 20 (120 m) | Smith and Walker (2002) |

[a] Based on 2–4 allozyme loci

[b] Based on seven microsatellite loci

same genet becomes extremely low due to the increased number of genets that occur as the dispersal area increases. The longest distance travelled by a single pollen grain has been estimated at 178 m. These pollen dispersal results for *P. australis* reflect a tail of dispersal that extends significantly beyond the mean (Kinlan et al. 2005; Hardy 2009). However, accurate characterization of dispersal kernals is extremely challenging (Nathan 2006), and particularly so in large, dense, variably clonal seagrass meadows that are probably experiencing significant immigration of pollen from outside the locally sampled meadow. A theoretical maximum pollen dispersal distance was estimated based on the length of time pollen grains are viable (up to 50 h) (Smith and Walker 2002) and water (current) velocities (Steedman and Craig 1983). The theoretical maximum pollen dispersal distance is 9 km in calm conditions and between 18 and 45 km during stormy conditions, based on an assumption that pollen grains were not entrained within a meadow due to boundary layer effects and synchronous leaf fluttering. This value is very difficult to confirm in the field, however, the co-occurrence of austral winter storms during peak pollen dehiscence (during August/September) could have a large effect on pollen dispersal distances for these seagrass species. Uninterrupted pollen transport based on local hydrodynamics can lead to dispersal distances of 70 m $h^{-1}$ and this can potentially lead to much larger dispersal distances (km) over the viability duration of pollen (days) (Verduin et al. 1996). Hydrodynamic modelling is indicating potential dispersal distances over 10's of km but measurements of the actual dispersal distances estimated from genetic analysis is much less. Further fine-scale and high intensity sampling is required to improve our understanding of the probability of successful pollen dispersal over a range of distances.

#### 6.4.1.2 Seed Dispersal in Posidonia

*Posidonia* species develop large buoyant dispersive fruit that contain a single negatively buoyant seed (Kuo and McComb 1989) (Fig. 6.3). The seed has no dormancy and is often referred to as a 'seedling' because it starts to grow a shoot and root radical while held within the dispersing fruit. At maturity, the fruit is released from the parent plant and floats rapidly to the water surface where it disperses under the effects of windage and water movement (Ruiz-Montoya et al. 2012) (Fig. 6.3). There is a vast range in annual seed production within and among meadows, with millions of seeds produced in some meadows (McMahon et al. 2014). Tracking dispersing fruit is difficult, and determining the point at which a seed is released (fruit dehiscence) is impossible to observe in situ. However, ex situ monitoring of time to dehiscence in tanks indicates that all fruit dehisced within six days after release from the parent plant (Ruiz-Montoya et al. 2012). The modelling of seed dispersal distance probability as well as survival of seedlings, predicted 0.01% of seeds released would travel up to 70 km and survive (McMahon et al. 2014), with some seeds likely to reach distances of 100 km from the source meadow every year (Ruiz-Montoya et al. 2015).

Three regional genetic studies of *P. australis* meadows (Perth metropolitan waters, New South Wales estuaries, south eastern Australia) have been conducted, with two key points emerging: genotypic diversity varies considerably among meadows within each region and the level of genetic differentiation ($F_{ST}$) also differs widely with each region (Evans et al. 2014; Sinclair et al. 2014b, 2016b) (Tables 6.4, 6.5 and Fig. 6.4). This highlights the significant role of sexual reproduction in maintaining most meadows (Table 6.4). This is not the case for meadows towards the range edge for the species and physically isolated meadows, which show a typical pattern of lower diversity, with some sampled meadows having less than 5 MLGs, and an overall average genotypic diversity of 0.22 in NSW (Evans et al. 2014) (Table 6.4). The genotypic diversity was much higher in meadows sampled from Perth metropolitan waters in Western Australia, overall $R = 0.63$ (Sinclair et al. 2014b), indicating more than half the ramets sampled were unique genotypes. Genotypic diversity among meadows within the Bass Strait was also considerably higher, $R = 0.54$ than northern NSW meadows. This implies that in these sites there is a greater contribution of sexual reproduction, rather than vegetative reproduction for population establishment and/or persistence.

Patterns of genetic connectivity and structure differ widely between these three regions, most likely reflecting the differences in historical and contemporary influences, complexity of coastlines, and the spatial scales of the studies. A detailed genetic study of meadows within the semi-enclosed Cockburn Sound, Western Australia, sampled 13 meadows over a distance of 40 km (Sinclair et al. 2014b). A significant isolation by distance (IBD) relationship was identified among meadows over approximately 16 km within the large protected water body of Cockburn Sound (Fig. 6.5). This relationship was not significant over larger spatial scales extending outside of the sound (Sinclair et al. 2014b) (Table 6.5 and Fig. 6.5), although most meadows were significantly differentiated based on pairwise $F_{ST}$ values (range from 0.015 to 0.162, overall $F_{ST} = 0.085$, $P < 0.001$) (Table 6.5). The subsequent development of a hydrodynamic model for the region (Ruiz-Montoya et al. 2015) shows this pattern of genetic differentiation is strongly driven by the effects of water and windage on the dispersing buoyant fruits (containing seeds). Most seeds are dispersed in a northerly direction with the prevailing winds and hence the ‘isolation by distance’ (IBD) relationship observed in the semi-enclosed system found in Cockburn Sound. Once fruits have dispersed

**Table 6.4** Demographic and genetic connectivity estimates for Australian seagrass via clonal growth and vegetative fragment dispersal

| Species | No. pops | No. samples | No. MLGs | Average genotypic diversity (*R*) (Min-Max) | Number shared MLGs among meadows | Max distance between shared MLGs (km) | Reference |
|---|---|---|---|---|---|---|---|
| **Posidoniaceae** | | | | | | | |
| *P. australis* | 13 | 621 | 393 | 0.63 (0.19–0.96) | 3 | 20 | Sinclair et al. (2014b) |
| *P. australis* | 12 | 360 | 79 | 0.22 (0.03–0.69) | 7 | 200 | Evans et al. (2014) |
| *P. australis* | 14 | 417 | 223 | 0.53 (0.24–0.96) | 0 | – | Sinclair et al. (2016b) |
| **Zosteraceae** | | | | | | | |
| *Z. muelleri* | 4 | 477 | 169 | 0.35 (0.04–0.65) | 0 | – | Sherman et al. (2016) |
| *Z. muelleri* | 14 | 482 | 306 | 0.67 (0.00–1.00) | 1 | 247 | van Dijk (unpublished data) |
| *H. nigricaulis* | 16 | 712 | 468 | 0.66 (0.09–0.91) | 4 | 20 | Jenkins et al. (2015) |
| **Hydrocharitaceae** | | | | | | | |
| *T. hemprichii* | 13 | 605 | 343 | 0.55 (0.09–0.94) | 26 | 34 | Hernawan (2016) |
| *T. hemprichii* | 12 | 478 | 273 | 0.56 (0.09–1.00) | 21 | 3 | van Dijk (unpublished data) |
| *H. ovalis* | 6 | 291 | 212 | 0.72 (0.16–0.96) | na | na | van Dijk (unpublished data), McMahon (2005) |

**Table 6.5** Indirect estimates of genetic structure for Australian seagrasses

| Species | No. pops | No. samples | Global $F_{ST}$ | Range in site pairwise $F_{ST}$ | Spatial scale (km) | Significant Isolation by distance | Reference |
|---|---|---|---|---|---|---|---|
| **Posidoniaceae** | | | | | | | |
| *P. australis* | 13 | 621 | 0.085 | 0.01–0.16 | 45 | Y but at smaller scale only | Sinclair et al. (2014b) |
| *P. australis* | 12 | 360 | 0.344 | 0.11–0.56 | 600 | Y | Evans et al. (2014) |
| *P. australis* | 14 | 417 | 0.254 | 0.02–0.32 | ~2000 | Y | Sinclair et al. (2016b) |
| **Zosteraceae** | | | | | | | |
| *Z. muelleri* | 4 | 477 | 0.278 | | 16 | N | Sherman et al. (2016) |
| *Z. muelleri* | 14 | 482 | 0.251 | 0.01–0.30 | 1488 | Y | van Dijk (unpublished data) |
| *H. nigricaulis* | 16 | 712 | 0.169 | | 55 | N | Jenkins et al. (2015) |
| **Hydrocharitaceae** | | | | | | | |
| *T. hemprichii* | 13 | 605 | 0.200 | 0.02–0.49 | 74 | N | Hernawan (2016) |
| *T. hemprichii* | 12 | 478 | 0.352 | 0.00–0.55 | 1132 | Y | van Dijk (unpublished data) |
| *H. ovalis* | 6 | 291 | 0.178 | 0.04–0.18 | 14 | na | (van Dijk, unpublished data), McMahon (2005) |

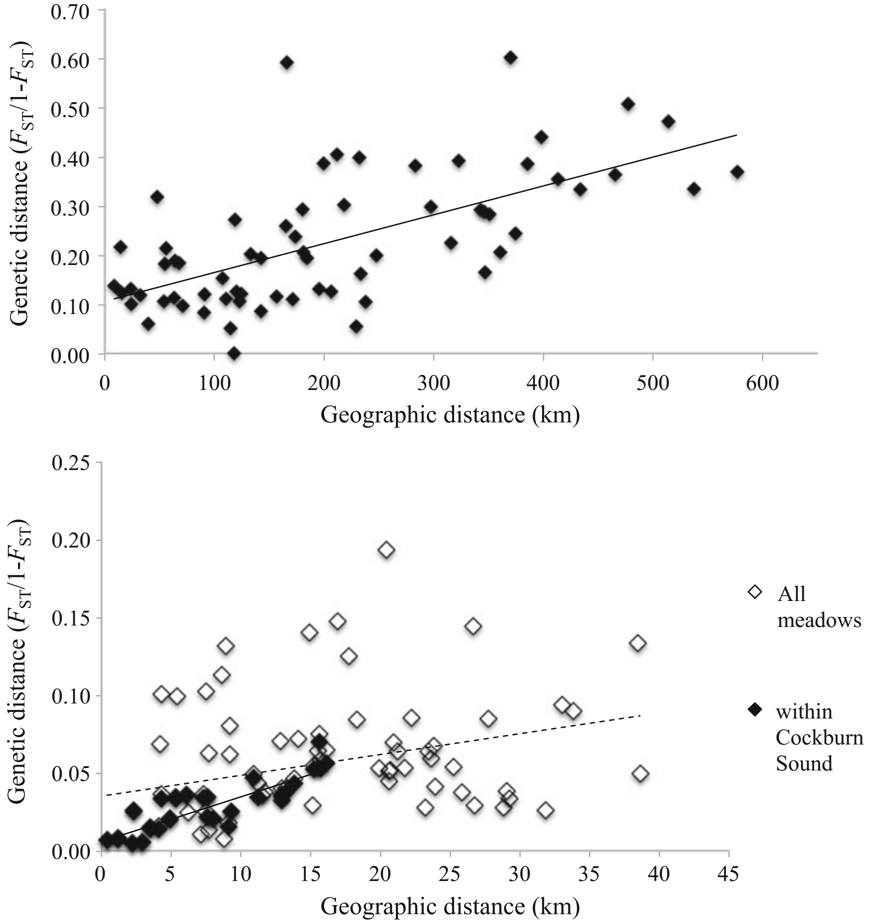

**Fig. 6.5** Testing the isolation by distance relationship: genetic distance ($F_{ST}$/1-$F_{ST}$) and geographic distance (km) for pairwise comparisons of *P. australis* meadows. **a** Along the New South Wales coastline (n = 12; Mantel test: $R^2 = 0.43$, $P < 0.001$) (Evans et al. 2014). **b** 13 Western Australian meadows across Perth Metropolitan coastal waters (dotted line, n = 13; Mantel test, $R^2 = 0.11$, $P = 0.085$) and meadows sampled within Cockburn Sound (solid line, n = 8; $R^2 = 0.72$, $P < 0.001$) (Sinclair et al. 2014b)

northwards outside the Sound, they may mix with fruit from many other meadows, and the IBD signal is weaker or lost.

Genetic structure among meadows in south eastern Australia is much higher than along the west coast, with $F_{ST}$ values of 0.163 ($p < 0.001$) among nine sampled meadows in the Bass Strait (Sinclair et al. 2016b) and 0.344 ($p < 0.001$) among NSW meadows (Evans et al. 2014). The Bass Strait meadows are strongly differentiated from meadows in South Australia and NSW. The very strong regional differentiation is consistent with long term barriers to dispersal persisting in the marine environment through many sea level fluctuations, while the Bass Strait Island meadows all have signals of genetic admixture. A weak but significant IBD relationship is consistent with contemporary seed dispersal probabilities developed with the aid of a hydrodynamic model (Sinclair et al. 2016b).

The genetic study of *P. australis* in NSW sampled 12 of the 14 known *P. australis* meadows along approximately 600 km of coastline, including the northern edge of the range (Evans et al. 2014). Unlike the more continuous meadows along the west coast, the east coast meadows are only found within protected soft-sediment estuaries and embayment's (West 1983). A much stronger IBD relationship was observed along the east coast (Mantel test: $R^2 = 0.43$, $p < 0.001$, Table 6.5 and Fig. 6.5), in which both allelic and genotypic diversity declined towards the northern edge of the range. The southern most meadows were significantly differentiated from the northern meadows, based on having a unique set of genotypes. The patterns in genetic diversity are explained by low levels of connectivity among estuaries, with limited dispersal from the south to the north due to the strong southward moving East Australian Current and the eddies which move propagules offshore.

#### 6.4.1.3 Dispersal and Gene Flow via Vegetative Fragments

*Posidonia* is one of a few seagrass genera in which vegetative recruitment has been documented. For at least two Australian *Posidonia* species, *P. australis* and *P. coriacea*, Campbell (2003) found that vegetative fragments recruited. However, this observation was possible due to the scale of the process observed, where erosion from local meadows and dispersal over meters was occurring. The observations made determined that *P. australis* recruits surviving greater than ten months began to show evidence for rhizome extension. This demonstrates that dispersal and survival of vegetative fragments, at least over scales of meters is possible. The patterns obtained from multiple sampling of the same genetic clones within meadows is consistent with clonal growth through rhizome extension, or local recruitment of vegetative fragments—there is no way to differentiate as clones also naturally become physically fragmented within a meadow over time. Vegetative fragments must disperse beyond the parent meadow and interbreed with a new gene pool for genetic connectivity to be realized. No research has been conducted to determine how successful vegetative fragments of *P. australis* are at dispersing and recruiting into new meadows. However, genetic data may provide some information on the success of vegetative dispersal in *P. australis* (i.e. through the sharing of multilocus genotypes between meadows). Examination of population genetic structure within 13 *P. australis* meadows across Cockburn Sound (Western Australia) (393 unique MLG's from 621 samples), found only three cases (<1% of MLG's) where a MLG was shared among meadows covering distances of 0.4, 16.1, and 20.6 km (Sinclair et al. 2014b) (Table 6.4). The sharing of MLGs was more extensive in northern NSW, with seven out of 79 MLGs (9%) shared over seven meadows, with most shared MLG's separated by 150 km, and three shared over 200 km (Evans et al. 2014).

Four possible explanations for sharing a MLG across meadows include (1) dispersal of vegetative fragment with successful recruitment into the new meadow, (2) two different plants having the same MLG (that is, two seed recruitment events each with the same MLG), (3) historical signature of a shared refuge during periods of lower sea level, and (4) a MLG is long lived and has grown to occupy a large area with time. It is very challenging to differentiate between these options. Campbell (2003) demonstrated that Option 1 is possible, but there is no direct evidence that this occurs between meadows for *P. australis*. It is unlikely that dispersal and recruitment of vegetative fragments plays a significant role in connectivity for *P. australis* meadows, due to the low number of shared MLG's detected among meadows. A mating system study showed that the set of genetic markers used were unable to differentiate all sexually-seeds produced within a sampled meadow; that is 3–7% of seeds shared an MLG with at least one other seed (Sinclair et al. 2014a). This indicates that Option 2 may be possible, but it could be that the genetic markers utilised did not differentiate genetically similar MLGs, rather than embryos having identical genotypes. Further mating system studies using additional markers providing greater resolution to eliminate a technical cause for this result are needed to resolve the uncertainty with this explanation. The aging of seagrass meadows is difficult, however, the ability to date sediment cores from seagrass matte (Serrano et al. 2016) may provide some insight in the future. Arnaud-Haond et al. (2012) estimated that Mediterranean *P. oceanica* clones could be over 200,000 years old. They also found shared MLG's across meadows in 3–8.5% of the MLG's identified. In the west coast example, the maximum distance among between shared MLG's was 20.6 km, if this was due to clonal growth the clone would be around 500,000 years old based on a growth rate of 4 cm/year$^{-1}$. Along the East Coast of Australia, due to current distribution of seagrasses within estuaries and bays and the lack of suitable habitat for coastal seagrasses, the shared MLG's could be the result of long-lived clones that previously shared glacial refugia during sea level fluctuations (Evans et al. 2014) which were up to 120–130 m below current levels. This is a more likely option than shared MLG's through contemporary dispersal of fragments over 200 km as the presence of the strong offshore southerly moving East Australian Current and associated eddies (Mata et al. 2006) are not conducive to extensive northward dispersal up the coast.

### *6.4.2 Case Study Australian* Zosteraceae

The Australian *Zosteraceae* consists of several widely distributed species, although the taxonomy of this group remains controversial. One of the most common and broadly distributed species is *Z. muelleri* (synonymous with *Z. capricorni*, *Z. nova-zealandica* and *Z. mucronata*), occurring in both Australia and New Zealand. This species is predominantly temperate, but extends into tropical waters on the

Australian east coast, and is found in protected estuaries and bays, both intertidally and subtidally (den Hartog 1970; West 1983). *Heterozostera tasmanica*, *H. nigricaulis* and *H. polychlamis* are also temperate species common to embayments and some open coastal environments, and tend to grow mostly subtidally (for the current status of the genus *Heterozostera*, see the Appendix). All Australian *Zosteraceae* are monoecious with annual production of flowers that develop in spathes of reproductive shoots. Male flowers tend to develop first within each spathe, followed by female flowers (Pettitt 1984). There is large temporal and spatial variability in flower production and reproductive effort, and seeds can accumulate in the sediment forming a dormant seed bank (Conacher et al. 1994; Jenkins et al. 2015). Seeds are negatively buoyant, but can be dispersed by the reproductive shoots that dislodge from the parent plant. There is also the potential for biotic dispersal of seeds and evidence for long distance dispersal of vegetative propagules within this group. There is no information on pollen dispersal in the Australian *Zosteraceae*, however, a number of studies have been published or are in review on the genetic connectivity of the Australian representatives of this family (Coyer et al. 2013; Macreadie et al. 2014; Jenkins et al. 2015; Thomson et al. 2015; Sherman et al. 2016) (van Dijk unpublished data) (Fig. 6.4).

#### 6.4.2.1 Dispersal of *Zosteraceae* Sexual Propagules

Flowers and seeds are produced annually in *Zosteraceae*, with the timing varying depending on the species and location (Inglis and Lincoln Smith 1988; Conacher et al. 1994; Campey et al. 2002; Jenkins et al. 2015). While there have been no direct estimates of seed dispersal distance in Australian *Zosteraceae*, their structure and morphology suggest they are likely to be similar to estimates for northern hemisphere *Zostera* (e.g. *Z. marina*), and limited to a few metres from the parental plant (Orth et al. 1994). This is consistent with surveys of the seed bank of *Z. muelleri* which show that seeds are largely retained within the seagrass meadow, with few seeds found in sediments surrounding meadows (Conacher et al. 1994). While seeds appear to have limited dispersal potential, long distance dispersal may be achieved via the rafting of reproductive shoots that fragment from the parent plant and are dispersed by ocean currents (Orth et al. 2006; Erftemeijer et al. 2008; Kallstrom et al. 2008). Dispersal of these reproductive shoots can potentially be very large but will be highly dependent on local hydrodynamic regimes (Harwell and Orth 2002; Reusch 2002; Kendrick et al. 2012). Dispersal via biotic vectors have not been widely studied in Australian *Zosteraceae*, however, recent research suggests that grazing turtles and dugongs may be important dispersal vectors in tropical seagrass meadows (Tol et al. 2015) (Table 6.2). Seeds of the northern hemisphere *Z. marina,* which has very similar seeds to Australian *Zostera and Heterozostera*, have also been shown to be dispersed by fish and turtles (Sumoski and Orth 2012; Tulipani and Lipcius 2014).

While there is a lack of studies on the dispersal potential of sexual propagules in Australian *Zosteraceae*, the development of microsatellite markers for two species

(Sherman et al. 2012; Smith et al. 2013) are now providing some insights into the relative importance of sexual and asexual reproduction in maintaining populations, and patterns of connectivity within and between seagrass meadows for at least two species, *Z. muelleri* and *H. nigricauli*s. Local studies on the genetic structure of *Z. muelleri* meadows have revealed varying levels of genotypic diversity, with some sites dominated by a small number of genotypes (genotypic diversity R = 0.04), while others show higher levels of genotypic diversity (R = 0.65) (Macreadie et al. 2014; Sherman et al. 2016) (Table 6.4). A larger-scale study of *Z. muelleri* along 1500 km's of coastline in north eastern Australia from Moreton Bay to Torres Strait, also found a large range in genotypic diversity from 0.01 to 1.0, with an average of 0.65 across the study (van Dijk, unpublished data). Similarly, *H. nigricaulis* shows high levels of variability in genotypic diversity, with genotypic diversity R ranging from 0.09 to 0.91 in surveys of several populations in Victoria and Tasmania (Jenkins et al. 2015) (Table 6.4). Jenkins et al. (2015) also reported a positive relationship between genotypic diversity and both seed bank density and spathe density in surveys from several sites within Port Phillip Bay, Victoria. These studies show that for both species, sexual propagules are important in maintaining populations and that levels of genotypic diversity can be strongly influenced by reproductive effort.

Estimates of connectivity within and between meadows in *Z. muelleri* and *H. nigricaulis* are highly variable, with significant genetic structuring detected across several spatial scales (Jenkins et al. 2015; Sherman et al. 2016, van Dijk, unpublished data) (Fig. 6.6). For example, estimates of connectivity in *Z. muelleri* within Australia's largest coastal saltwater lake (Lake Macquarie) revealed that significant genetic structure exists among locations separated by up to 16 km with a global $F_{ST} = 0.278$ ($P < 0.0001$) (Table 6.5). The hierarchical sampling of these locations also reveal that a significant proportion of this genetic variance was due to differences between replicate sites within locations (average $F_{ST}$ among sites within locations = 0.175 $p < 0.0001$), suggesting structuring at the tens to hundreds of metres scale (Sherman et al. 2016) (Table 6.5). At a larger scale along the Queensland coast similar levels of genetic differentiation were detected, the global $F_{ST} = 0.251$ ($P = 0.001$), highlighting that increasing distance between sites, does not necessarily result in an increase in genetic differentiation, as different processes may be operating (van Dijk, unpublished data). In this Queensland example, the pair-wise comparisons ranged from $F_{ST} = 0.01$–0.30, not that dissimilar to comparisons between sites in the embayment example described above. The lower levels of genetic differentiation ($F_{ST} < 0.001$) were observed between sites separated by up to 200 km, whereas the higher levels of genetic differentiation ($F_{ST} = 0.30$) were observed between sites separated by a minimum of 450 km (Table 6.5). This indicates that genetic connectivity is generally high in the coastal intertidal meadows along the Queensland coast over distances of up to 200 km, and is supported by migration estimates that show a high level of migration over distances of 12 km, with moderate levels over 8–160 km (van Dijk, unpublished data). This is in contrast to the situation in temperate Australia where meadows are located in large embayments, estuaries and lakes, and dispersal between these features may be more limited.

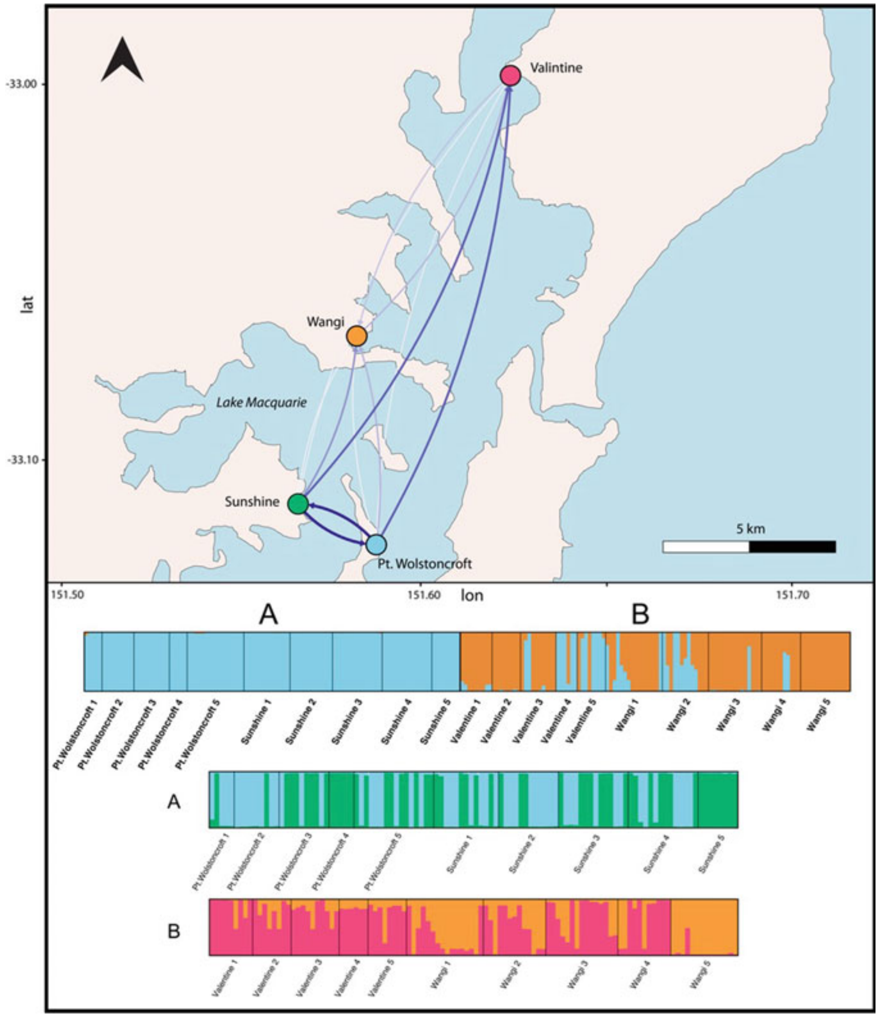

**Fig. 6.6** Patterns of connectivity and genetic structure in *Zostera muelleri* over a small spatial scale in Lake Macquarie (top) (Sherman et al. 2016) and a broad spatial scale along the Queensland coast (bottom) (van Dijk, unpublished data). Lines between sites show the estimated relative migration between sites. The coloured plots at the bottom of the graph show the spatial distribution of significant genetic grouping that were identified. For the Lake Macquarie case-study the genetic structure occurs over a number of spatial scale and for the Queensland case-study both two (K = 2) and six (K = 6) genetic groupings were strongly supported. The colour of the site location dots on the map relate to the colours on the structure plot

Estimates of genetic differentiation within a large Victorian embayment, Port Phillip Bay, for *H. nigricaulis*, showed high levels of genetic differentiation among locations separated by up to 55 km ($F_{ST} = 0.169$), while estimates between sites within meadows separated by 20–50 m were much lower ($F_{ST} = 0.070$)

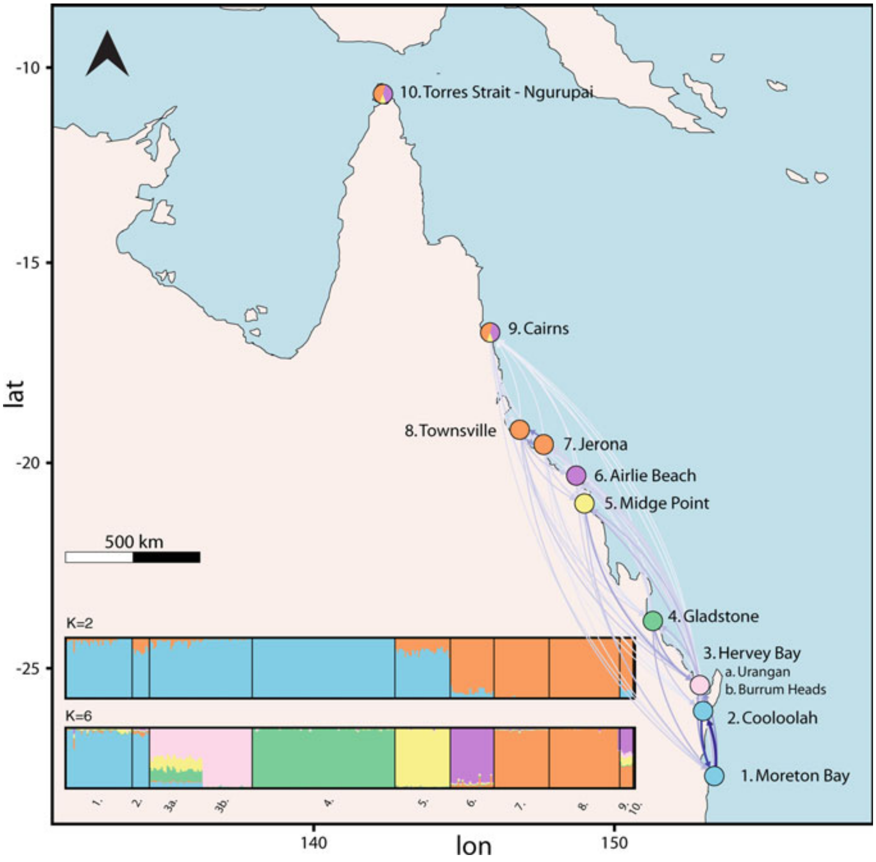

**Fig. 6.6** (continued)

(Jenkins et al. 2015) (Table 6.5). This is similar to that reported for the temperate *Z. muelleri* (Sherman et al. 2016). The significant genetic structuring at even fine spatial scales in both species suggests that sexual propagules are largely retained locally within seagrass meadows in large embayment populations. These studies also found that patterns of genetic connectivity within local embayments (e.g. populations separated by between 5 and 55 km) rarely follow any pattern of isolation by distance (i.e. when neighbouring populations are more likely to be connected by gene flow compared to more geographically distant populations). This is likely to result from complex local hydrodynamic regimes that do not result in geographic distance being a good predictor of genetic connectivity between populations. Better integration of genetic data, life history traits and hydrodynamic dispersal models is required.

In a broader perspective significant Isolation By Distance (IBD) was found along the Queensland coast covering a range of 1488 km and 32% of the variation could be attributed to IBD (van Dijk, unpublished data). This resembles the case with the coastal versus estuarine *Posidonia* example, there is greater potential for oceanographic connectivity of coastal seagrass meadows along the Queensland coast, and this may explain the larger spatial scale of genetic connectivity observed.

#### 6.4.2.2 Dispersal of Vegetative Propagules

The rhizome fragments and clonal propagules of *Z. muelleri* and *H. nigricaulis* appear to be adapted for long distance dispersal and are likely to be an important mechanism for maintaining connectivity both locally (i.e. within meadows) and potentially between distant meadows (Kendrick et al. 2012; McMahon et al. 2014; Stafford-Bell et al. 2015; Thomson et al. 2015). Clonal propagules may also provide a mechanism for rare extremely long distance dispersal (e.g. trans-oceanic dispersal events) and the establishment of new meadows (Harwell and Orth 2002; Reusch 2002; Coyer et al. 2013; Thomson et al. 2015).

Studies on the buoyancy and viability of *Z. muelleri* and *H. nigricaulis* fragments indicate that they actively grow and remain viable for 10–12 weeks after detachment. The survival and recruitment of these propagules is low, however, given the vast numbers of fragments produced, even rare recruitment events are likely to make an important contribution to population maintenance and connectivity (Stafford-Bell et al. 2015; Thomson et al. 2015). In *H. nigricaulis*, genetic surveys of several meadows in Port Phillip Bay, Victoria, have detected the sharing of a small number of multilocus genotypes between meadows separated by up to 20 km's. However, for *Z. muelleri*, a study in Australia's largest coastal lake, Lake Macquarie, found no sharing of genotypes between meadows separated by 10–16 km's Sherman et al. (2016), and only 1 over a distance of 247 km between meadows on the Queensland coast (van Dijk, unpublished data), although lack of marker resolution cannot be excluded. While these studies have only shown a small number of shared genotypes between meadows, there is greater sharing of genotypes between sites within meadows (ten's of metres). For example, Sherman et al. (2016) found between 1 and 3 MLG shared between two to three sites within a meadow for *Z. muelleri* (Table 6.5). The sharing of MLG among sites within meadows may arise from localised dispersal and recruitment of clonal propagules over tens to hundreds of metres, but may also result from rhizome extension over long periods.

### 6.4.3 *Case Study* Halophila ovalis

*Halophila ovalis* is one of the most widely geographically distributed seagrass species, growing in tropical and temperate waters and the smallest seagrass genera, with easily recognizable oval-shaped leaves. It is dioecious, male and female flowers form on separate plants, arising directly from between the leaves on the rhizome. Pollen is released at the top of the canopy by male flowers and the female flowers have long styles, extending above the canopy, which capture pollen (Fig. 6.1). Once pollinated, small fruits (3–5 mm) develop either just above or below the sediment, containing up to 15 seeds, 0.5–2.0 mm in diameter (Fig. 6.2). The seeds are negatively buoyant and have a dormancy period of up to 2 years (Kuo and Kirkman 1992).

There are no studies on pollen-mediated gene flow in *H. ovalis*, but pollen movement through and at times, along the surface of the water (Fig. 6.1) occurs where it will be intercepted by the stigmas of the female flowers. Seeds will not travel far once settled in the sediment unless sediment movement as a whole occurs leading to secondary dispersal when seeds are resuspended with sediment under high turbulence conditions, such as in storms (Kendrick et al. 2012). Dispersal of fruits has not been documented so far in literature, but it is very likely that fruits disperse when still attached to dislodged rhizomes (e.g. Figure 6.2). Herbivore-mediated dispersal has also been suggested (Kendrick et al. 2012; McMahon et al. 2014), and viable *H. ovalis* seeds have been observed in dugong faeces (Tol et al. 2015) as well as fish and birds (Wu et al. 2016) (Table 6.2), but the significance of this dispersal process is unknown. Wu et al. (2016) suggest that dispersal by birds is likely to be longer due to the longer passage time through the gut and greater distances moved by birds.

Very few population genetic studies have been undertaken for *H. ovalis*. A recent study presented ten polymorphic microsatellites (Nguyen et al. 2014), but successful amplification of all loci has been limited. The study of a large potentially highly connected system in Moreton Bay (Queensland, van Dijk unpublished data) found that dispersal was not high among the major areas sampled. Indeed, this study found that significant genetic structure was present within, over a distance of 16 km (Fig. 6.4). A global $F_{ST}$ value of 0.178 was found with pairwise $F_{ST}$ values ranging between 0.009 and 0.185 for the six populations tested (Table 6.5). Population assignment analysis (using Structure Bayesian modelling) identified 2 or 4 significant population clusters within the study area. Genotypic diversity ranged from $R = 0.16$–$0.96$, with 4 of the 6 sites greater than 0.8 (Table 6.4). This highlights that in general sexual reproduction is important for maintaining populations, but in some cases clonal reproduction rather than sexual reproduction is more important for population persistence. New recruits were estimated to be most likely sourced from within a meadow (71–90% of individuals), compared to migration from other meadows (3–17% of individuals), and were migration occurred it was greatest over distances of 1–5 km (Fig. 6.7). There was no evidence that dugongs were facilitating significant dispersal of seeds due to the low levels of migration and high genetic differentiation among sampled meadows (McMahon 2005) (van Dijk unpublished data).

### 6.4.4 *Case Study* Thalassia hemprichii

*Thalassia hemprichii* is a tropical species extending from Exmouth, Western Australia to Magnetic Island (Queensland) on the east coast of Australia. It is dioecious, with male and female flowers on separate plants, both forming at the

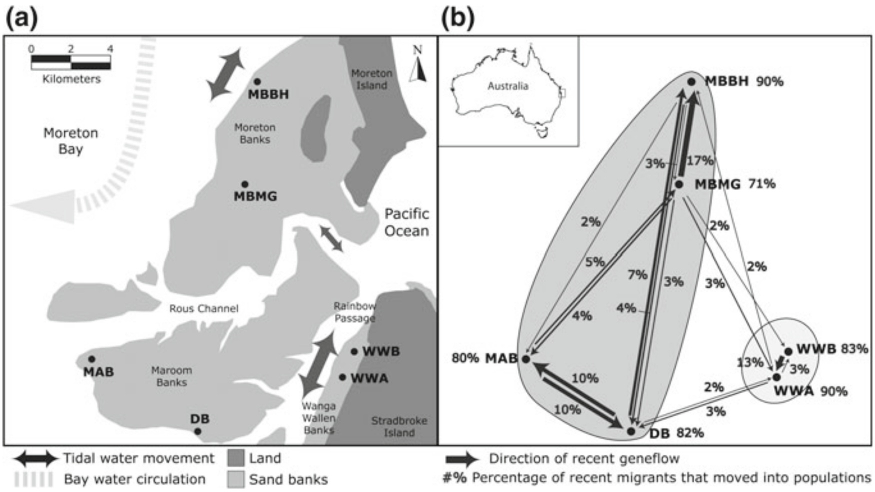

**Fig. 6.7** Estimates of demographic connectivity and migration between meadows for *H. ovalis* in Moreton Bay based on Bayesian modelling. **a** Location of the six study sites on the eastern banks of Moreton Bay, Australia (Moreton Banks: MBBH, MBMG, Maroom Banks: MAB, DB, Wanga Wallen Banks: WWB, WWA). **b** Shaded areas visualize the two genetic clusters composed of multiple populations according to the Bayesian assignment test under K = 2 with STRUCTURE. Arrows represent the level of contemporary migration (direct migrants or F1 of migrants) into populations; the percentages are the fraction of MLGs that moved into the population (McMahon 2005) (van Dijk, unpublished data)

base of the shoot. Buoyant fruits form, which can disperse, and following fruit dehiscence the negatively buoyant seeds sink (Lacap et al. 2002; Wu et al. 2016). There is no dormancy period in the seeds, so they develop as soon as they are released (Kuo et al. 1991), sometimes already forming leaves by the time the fruit splits to allow them to escape (Jane Mellors personal observation, Torres Strait). No detailed studies of flowering and fruiting of *T. hemprichii* have occurred in Australia. Vegetative fragments with only one node are buoyant for up to four weeks, and these can successfully recruit so there is potential for long distance dispersal with this mechanism (Wu et al. 2016). No studies on pollen dispersal have been undertaken on this species.

#### 6.4.4.1 Dispersal of Sexual Propagules

Waycott et al. (2004) collated flowering observations, and identified a peak flowering time in June-September in north eastern Australia, although this may vary in other places, such as the west coast of WA. As fruit production is likely seasonal, dispersal of these reproductive propagules would occur in particular months of the year. The fruits are an excellent means for dispersal (Kuo et al. 1991) as long as the fruit is released from the plant before dehiscence. Detached mature fruits remain afloat for between 1 and 7 days (Lacap et al. 2002; Wu et al. 2016) with a dispersal distance of 23–74 km in the Bolinao Reef system, Philippines (Lacap et al. 2002). The seeds of *T. hemprichii* have relatively limited dispersal capacity compared to the fruits because they immediately sink once released from the fruits and they have no dormancy period (Kuo et al. 1991; Rollon et al. 2003). However, some seedlings can float, potentially due to oxygen accumulation in the lacunae, for 27–38 days, providing another dispersal mechanism (Wu et al. 2016).

The genetic diversity and connectivity among Australian *T. hemprichii* populations has been evaluated in two studies to date; one at a local scale from 13 meadows in the Kimberley, Western Australia, over two islands groups with sites ranging from 2 to 73 km apart (Hernawan 2016), and the other along the coast of Queensland spanning 12 meadows over 1132 km, to the southern edge of the Australian east coast distribution (van Dijk, unpublished data) (Table 6.5 and Fig. 6.4). The level of genotypic diversity within meadows varied considerably in both studies from R = 0.09–0.94 (Hernawan 2016) and R = 0.09–1.0 (van Dijk, unpublished data), indicating sexual reproduction is important for maintaining populations and that clonal growth and/or vegetative recruitment also contributes significantly to population structure, varying significantly among sites. For example in one location in the Kimberley only five unique MLGs were identified from 48 ramets genotyped ($R = 0.09$), and along the Queensland coast at the range edge only one individual was detected, and genotypic diversity declined towards the range edge (Table 6.4), similar to that which has been described for *P. australis* on the east coast (section above).

In the Kimberley, where all meadows are intertidal, and there are extreme tides (up to 11 m range) and complex hydrodynamics, there was significant genetic differentiation among all sites (global $F_{ST} = 0.201$, $P = 0.001$) and pairs of sites pairwise $F_{ST}$, ranging from 0.022 to more than 0.495, even over this small spatial scale (Hernawan 2016) (Table 6.5 and Fig. 6.8). This was supported in a STRUCTURE analysis where two significant spatially and genetically distinct clusters were detected. Yet, this genetic structure was not associated with the two island groups, in fact a significant barrier was detected within an island group, over a distance of 12 km. The patterns in genetic differentiation were best explained by the oceanographic connectivity between sites and the habitat at a site, specifically sediment type, and not by geographic distance (Hernawan 2016). Moderate levels of migration were detected over distances up to 45 km.

Genetic differentiation among all sites in the Queensland example was higher again, the global $F_{ST}$ was 0.352, as would be expected over this larger spatial scale (van Dijk, unpublished data). The site pairwise $F_{ST}$ ranged from 0.00 to 0.55, with the low $F_{ST}$ values (<0.10) occurring between sites over distances up to 200 km, and the upper end (>0.35) of the range occurring over distances at a minimum of 350 km. There was significant genetic structure over these sites, with a clustering of sites in the Torres Straits, an admixture zone around Lizard Island, and another cluster from the Low Isles southwards (Fig. 6.8). Isolation by distance was significant and explained 30% of the variation in genetic differentiation (van Dijk, unpublished data).

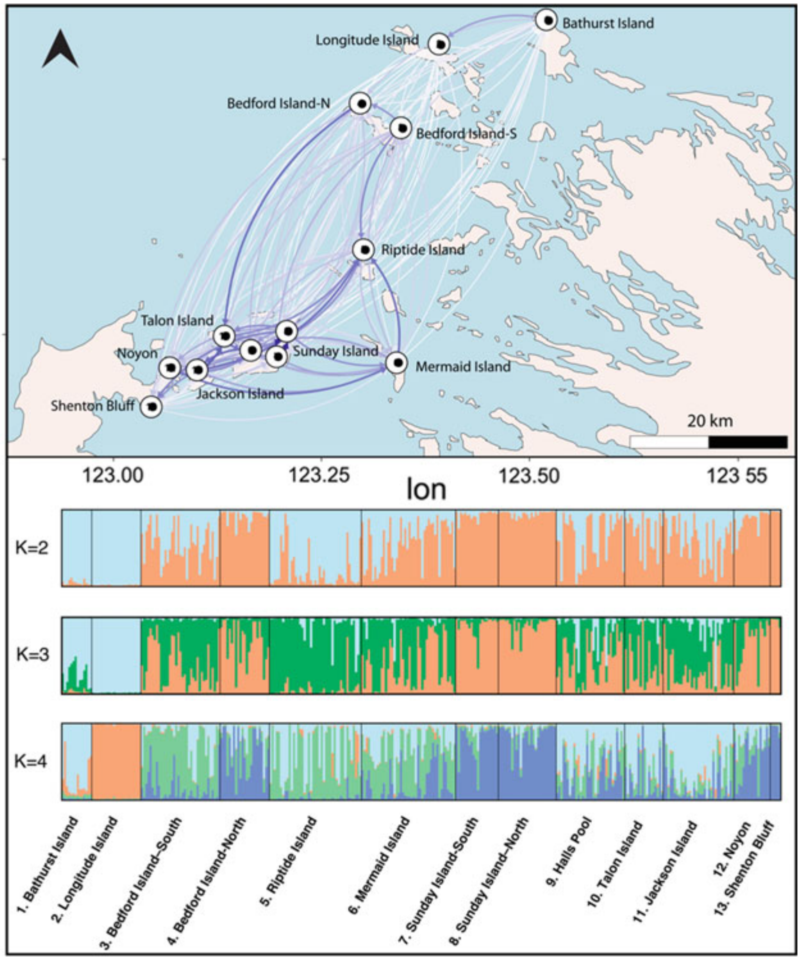

**Fig. 6.8** Patterns of connectivity and genetic structure in *Thalassia hemprichii* over a small spatial scale in the Kimberley, WA (top) (Hernawan 2016) and a broad spatial scale along the Queensland coast (bottom) (van Dijk, unpublished data). Lines between sites show the estimated relative migration between sites based on. The coloured plots at the bottom of the graph show the spatial distribution of significant genetic grouping that were identified. For the Kimberley case-study two to four genetic groupings are supported and for the Queensland case-study both two (K = 2) and five (K = 6) genetic groupings were strongly supported. The colour of the site location dots on the map relate to the colours on the structure plot

### 6.4.4.2 Dispersal of Vegetative Propagules

There are no data on the fragmentation rate of vegetative fragments, although this has been observed in some locations (Wu et al. 2016). But once generated, vegetative fragments can float and survive much longer than fruits and seedlings.

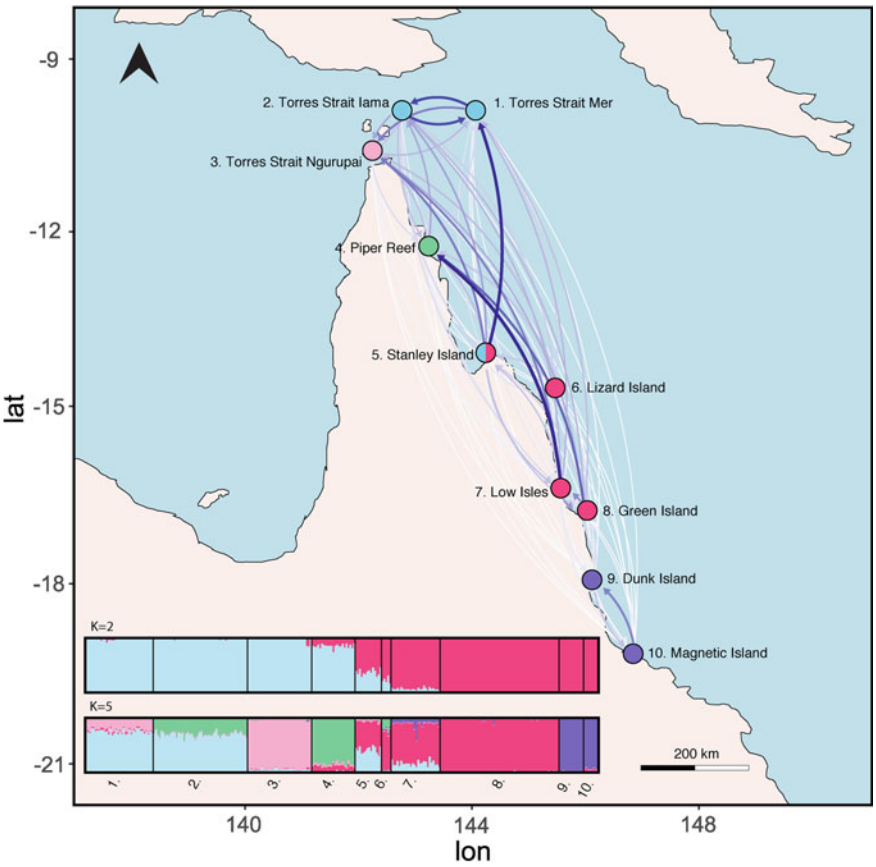

Fig. 6.8 (continued)

Seventy two percent of vegetative fragments with only one node survived and floated for four weeks with 17% still alive after 12 weeks (Wu et al. 2016). Re-analysis of data from the Kimberley found around 8% of MLG's (26 out of 343) were shared among meadows from distances of 2 km to a maximum distance of 34 km (Hernawan 2016). A similar percentage of shared MLGs was also detected among meadows in the Great Barrier Reef, although they were shared up to a maximum distance of 3 km (van Dijk, unpublished data) (Table 6.4). The sharing of MLGs among meadows may indicate either successful vegetative dispersal or extremely large clones that are long-lived.

## 6.5 Key Gaps in Our Knowledge

Our understanding of demographic and genetic connectivity of Australian seagrass meadows has greatly improved over the last decade, largely driven by the development of highly polymorphic genetic markers, reduction in cost and increase in the infrastructure enabling researchers to undertake this research. This increased investment has allowed us to start to examine the magnitude of genetic connectivity in seagrasses, and the drivers of connectivity among species and locations, although there is limited work on fine-scale patterns within meadows. Despite this, there are some clear gaps where we should focus future research.

A limited number of Australian species have been studied. Only five of the currently recognised 38 described seagrass species in Australia, have been studied in any detail. Genetic markers have been developed for additional species, so there are opportunities and ongoing research to improve this. Among those studied only *H. ovalis* does not have a floating dispersal phase, whereas the others have buoyant fruits (*Posidonia*, *Thalassia*) or floating reproductive shoots (*Zostera* and *Heterozostera*). Therefore, we do not have the ability to compare how different life history traits influence dispersal at this time. Finally, our understanding of species wide processes is based on sampling across a limited spatial range, limiting inferences.

Disentangling the relative importance of demographic and genetic connectivity of seagrasses over ecological timescales relevant for management is very challenging and a number of researchers are attempting this by combining a variety of approaches as proposed by Kendrick et al. (2017). Characterisation of population structure over a range of spatial and temporal scales and combining these results with demographic studies and modelling will assist in improving our understanding, and hence our ability to effectively manage and conserve seagrass habitat.

Other key knowledge gaps to help understand the significance of the different potential mechanisms of gene flow include:

- dispersal kernals of the different life-history stages of seagrasses that can disperse including the probability and success of transitions such as pollination, recruitment and survival of seeds linked with fitness measures;
- reproductive biology of Australian seagrass species—when do they release pollen, when do they release seeds, how long are the seeds viable for;
- physical properties for modelling dispersal in both the water and sediment, including the timing of release as described above, longevity of pollen and seeds as well as buoyancy;
- role of biotic dispersal, especially birds.

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# Part IV
# Ecology

# Chapter 7
# Seagrass Dynamics and Resilience

**Rod M. Connolly, Emma L. Jackson, Peter I. Macreadie,**
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**Abstract** The vulnerability of seagrass ecosystems, and the services they provide, to damage and loss from anthropogenic stressors has led to a surge of interest in understanding their resilience. This chapter examines patterns of change in tropical and temperate Australian seagrasses to identify underlying causes of the observed patterns. It then relates seagrass dynamics to ecosystem resilience, and examines how resilience can be measured, managed and enhanced. Seagrasses in tropical waters show strong seasonal patterns in many places, with seagrass extent and cover increasing during the winter dry season and decreasing during the summer wet season. This seasonality is overlaid by a striking longer term trend of increase during El Niño periods and subsequent loss during wetter, stormier La Niña periods. Seasonality is less evident in temperate waters, where mapping of dynamics has generally been used to show longer term patterns, especially large-scale loss after decades of stability, sometimes with partial recovery. Changes in some places have been linear and in others strongly non-linear, possibly indicative of systems breaching a threshold or tipping point in levels of stressors such as pollutants.

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Resilience theory has become a powerful tool for understanding the dynamics of seagrass change. Seagrass resilience requires several key traits: genetic and species diversity, good water quality, connected ecosystems and continuous habitats, and balanced trophic interactions. These traits are integrated through ecological feedbacks. In *Zostera muelleri* meadows, for example, the capacity for seagrass to resist decline during pulses of poor water quality depends on its ability to: (1) efficiently remove excessive nutrients from the water, thereby limiting phytoplankton growth and improving water clarity, (2) suppress resuspension of sediment for improved water clarity, and (3) provide habitat for grazing animals that remove epiphytic algae. The increased understanding of resilience is shifting the focus of seagrass ecosystem management towards the management of stressors to optimise key feedbacks, and thus ultimately to enhance resilience. The chapter culminates in descriptions of practical management actions demonstrated to effectively enhance key traits and overall seagrass resilience.

## 7.1 Introduction

Seagrasses provide ecosystem services and structure ecological processes in the nearshore coastal environment, which has led to a high level of interest from managers and scientists. We therefore have a large body of knowledge about the dynamics of seagrass presence and cover. Some populations (and species) are relatively persistent whereas others are dynamic over time and large areas have been lost. These differences are due to how seagrasses respond to environmental pressures and the different responses may be due to differences in resilience. This chapter examines patterns of change in tropical and temperate Australian seagrasses using case studies to identify some of the underlying causes of the observed patterns. It then reviews how the dynamics of seagrass in Australia relate to ecosystem resilience, and how resilience might be measured and enhanced.

### *7.1.1* Application of Resilience Theory to Seagrass

Resilience theory is becoming the cornerstone for developing predictive science in the field of ecology (Hughes et al. 2005), and the lens through which climate change adaptation is assessed (Visser 2008). In a broad sense, resilience refers to the capacity of an ecosystem to cope with disturbance. Environmental stressors can lead to an ecosystem shift from one state to another, and resilience is about an ecosystem's ability to remain in its current state. If the factors that provide resilience to a given ecosystem can be predicted, monitored and modified, we have the best chance of maintaining desired ecosystem states in the face of increasing environmental change (Folke et al. 2004). The understanding of mechanisms that confer ecosystem resilience and the development of resilience theory are two of the major challenges currently facing ecologists (Thrush et al. 2009).

Like many other coastal ecosystems, seagrasses are subject to multiple interacting stressors, including climate change, invasive species, coastal development, and eutrophication (York et al. 2017). Seagrass ecosystems are well-suited for developing an understanding of the mechanisms that underpin ecological resilience. Because they are typically the first habitats in nearshore waters to respond to environmental disturbance, they are often considered the 'canaries in the coalmine' of coastal ecosystems. Australia's National Climate Change Adaptation Research Facility has earmarked seagrasses as sentinels for the changing marine ecosystems of Australian coastal waters (Connolly 2012). Climate change is predicted to cause major loss of seagrass habitat directly, e.g. through physical removal during storms that are predicted to become more frequent, and indirectly, e.g. through degradation of abiotic conditions associated with rising sea levels, increasing water temperatures, and changes in salinity from altered rainfall patterns (Connolly 2012).

Seagrasses show variable adaptations for resistance to and recovery from disturbance. Resistance to short-term disturbances in the light climate is, for example, aided by the storage of carbohydrate reserves in some species (Fraser et al. 2014), or photo-adaptive and photo-protective responses in others (Campbell et al. 2007). Resilience is also enhanced by the existence of asexual and sexual recovery mechanisms, which include fast growth rates (Macreadie et al. 2014a), the stimulation of apex production (e.g. Eklöf et al. 2010), the existence of extensive seed banks (York et al. 2015) and the potential for propagules (seeds and vegetative fragments) to be transported from neighbouring meadows (McMahon et al. 2014; Stafford-Bell et al. 2015). The system traits underpinning seagrass resilience have been categorised in a resilience framework (Table 7.1; Unsworth et al. 2015). The role of ecological feedbacks is a central tenet of resilience, both feedbacks that help maintain seagrass growth, and those that prevent return to seagrass once lost. Because seagrasses are ecosystem engineers, the feedbacks evident [for example in terms of turbidity reduction and sediment stabilisation, Maxwell et al. (2014)] are important elements for consideration when examining how much disturbance can be absorbed before a state change (regime shift) is observed (Folke et al. 2004).

## 7.2 Seagrass Dynamics in Australia

### *7.2.1 Tropical Waters*

Tropical Australian seagrass meadows are highly dynamic (Birch and Birch 1984), with a dominance of transitory meadows of opportunistic and colonising seagrass species (Kilminster et al. 2015). Offshore, deep-water *Halophila* species are ephemeral as they are vulnerable to disturbance but can exhibit fast recovery from seed banks (Rasheed et al. 2014), a possible adaptation to the highly variable light

**Table 7.1** Seagrass resilience traits, management actions and practical methods that have been used to increase resilience of seagrass ecosystems (modified from Unsworth et al. 2015)

| Trait | Action | Method |
|---|---|---|
| Diversity—species and genetic | Increase genetic diversity | Deploy seeds from a wider region<br>Enhance genetic connectivity |
| Good water quality | Reduce physical impacts | Local management to avoid direct impacts such as anchoring and bait digging |
| | Reduce algal overgrowth | Improve water quality and manage fisheries to increase herbivory in the food web |
| | Increase photosynthetic productivity | Improve water quality |
| | Reduce chemical toxicity | Control entry into waterways of chemical toxicants |
| | Increase compliance with environmental regulations relating to seagrass | Improve local knowledge of the locations of seagrass meadows and their value and sensitivities |
| Connected ecosystems and continuous habitat | Reconnect isolated and fragmented meadows | Targeted restoration |
| | Maintain connectivity | Ensure continued presence and health of associated habitats (e.g. reefs, mangroves) |
| Balanced trophic interactions | Encourage balanced herbivory and bioturbation | Manage fisheries species, including predators, through fisheries and habitat management (e.g. marine reserves) |
| | Provide early warning of issues of concern | Monitoring of structure and functions linked to feedbacks |

environment to which these meadows are exposed. More stable seagrass meadows dominate shallower inshore waters in locations where physical disturbance is minimal. These meadows consist of species with more persistent life history traits, e.g. *Halodule uninervis* and *Zostera muelleri*, that rely primarily on vegetative clonal growth and are slower to recover from disturbance (Rasheed et al. (2014), although there is also one clear example of recovery through seed germination in Hervey Bay (Campbell and McKenzie 2004).

Despite inherent variability, long-term monitoring programs across tropical and subtropical Queensland have identified some intra- and inter-annual patterns in seagrass loss and natural recovery [for details of monitoring programs see Coles et al. (2015)]. The main drivers of seagrass dynamics in Queensland are tropical summer storms and cyclones, and associated flood events, which can cause large-scale losses (Poiner et al. 1989; Preen et al. 1995; Campbell and McKenzie 2004; York et al. 2015). Such events are highly seasonal and in many places an approximately two-fold change in seagrass standing crop between summer and winter has been observed (Young and Kirkman 1975; Lanyon and Marsh 1995;

York et al. 2015). The magnitude of seasonal change varies with latitude and species, e.g. York et al. (2015) observed a complete absence of seagrass between January and June at Hay Point, Queensland, whereas further north, seasonal patterns exist, but seagrass is generally present year round (Coles et al. 2015).

Pronounced seasonal cycles in seagrass meadows are evident even in years without extreme storm or flood events and have been linked to the following factors: day length and daytime air exposure for intertidal meadows (Mellors et al. 1993; Lanyon and Marsh 1995; McKenzie and Unsworth 2009; Rasheed and Unsworth 2011; Unsworth et al. 2015), water temperature (Mellors et al. 1993; Lanyon and Marsh 1995), rainfall and river flow (Lanyon and Marsh 1995), and wind strength and direction (Lanyon and Marsh 1995; Mellors et al. 1993). Rasheed and Unsworth (2011) analysed the temporal dynamics of an intertidal meadow of *Halodule uninervis* growing in turbid conditions over a 16-year period (Fig. 7.1). Variability in seagrass biomass was highly correlated with river flow (positive), air temperature (negative) and long-term cycles of tidal exposure. The study highlighted that whilst frequent flood events may decrease seagrass cover, too little rain (and the subsequent lack of river flow that supplies important nutrients) can also have a negative impact.

Longer-term dynamics are often driven by climate. For example, the frequency and magnitude of extreme storms and flood events are correlated with the El Nino

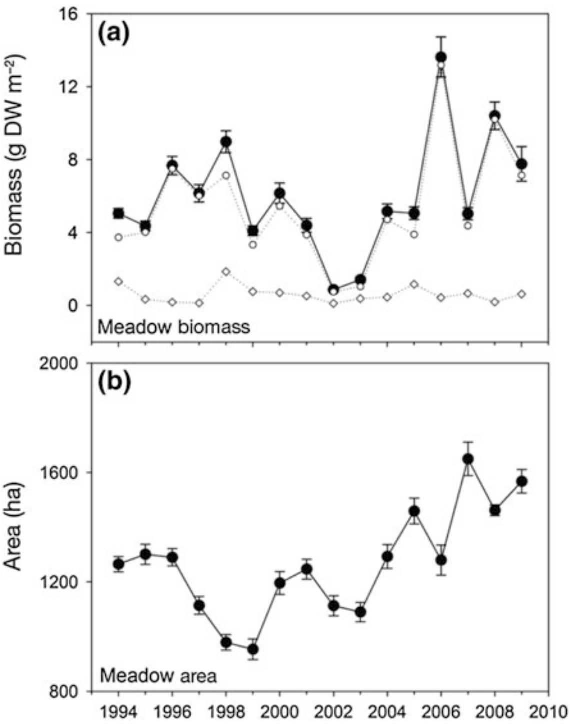

**Fig. 7.1** Dynamic change in seagrass biomass and area at Karumba (northern Queensland) over a 16-year period, Oct 1994–Oct 2009 inclusive (mean, SE). For biomass, bold line is total, dashed lines represent the two main species *Halodule uninervis* (upper line) and *Halophila ovalis* (lower line). From Rasheed and Unsworth (2011)

Southern Oscillation (ENSO). Above-average rainfall and more frequent storms and cyclones associated with La Niña events increase turbidity, decrease salinity and cause physical disturbance to the plants and seed banks, together resulting in large-scale declines of seagrass (Fig. 7.2). The combination of the 2010–11 La Niña event, one of the strongest on record, *and* the series of La Niña weather events in preceding years, exposing the region to above average rainfall and intense storm and cyclone activity, appears to have been the cause of the decline in seagrass cover across the Great Barrier Reef World Heritage Area (Coles et al. 2015; McKenna et al. 2015). Multiple years of La Niña may denude seed banks, and impede asexual revegetation.

Natural seasonal and inter-annual cycles in seagrass standing crop are subject to disruption due to direct anthropogenic activities and indirect climate effects (Grech et al. 2011; Saunders et al. 2015). Observations of deep-water seagrass meadows (primarily *Halophila decipiens* with marginal *H. spinulosa*) at Hay Point (Queensland) over an eight year period (York et al. 2015) identified strong annual seasonality, with seagrass present only between July and December each year. During 2006, no seagrass was present, which was attributed to persistent large-scale plumes of turbid water resulting from an eight-month dredging program. Recruitment occurred the next year and the annual cycle resumed, although biomass did not return to pre-dredge levels at any time during the study period (six years post-dredging) (York et al. 2015). It has been proposed that these tropical meadows, which are typically subjected to chronic stress in the form of seasonal storm disturbance, possibly in combination with intense grazing, have adapted to recover quickly not only from chronic stresses but also large acute disturbances (Unsworth et al. 2015).

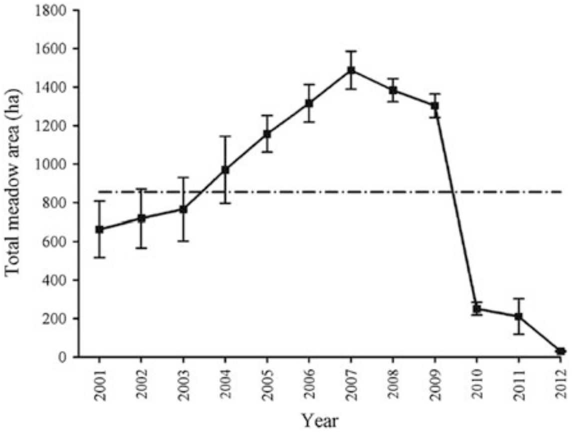

**Fig. 7.2** Dynamic change in area of seagrass meadows in Cairns harbour (northern Queensland), over a 12-year period, 2001–2012 (mean, SE). Dashed line represents long-term mean. From McKenna et al. (2015). Major La Niña-related weather event occurred 2010/2011

### 7.2.2 Temperate Waters

Australia's temperate seagrasses occupy southern waters from Shark Bay on the west coast to northern New South Wales on the east coast (see Chaps. 2 and 3). The diversity of Australia's temperate seagrasses is impressive. Approximately half of the 72 species that exist worldwide occur within Australia's southern waters, with a high degree of endemism and with it some unique plant characteristics (morphology and physiology—see Chap. 4) that reflect adaption to local environmental conditions.

Dynamics of eelgrass, *Heterozostera nigricaulis*, in Port Phillip Bay has been studied intensively in recent years (Macreadie et al. 2010; Jenkins et al. 2015; Hirst et al. 2016). This has resulted in a comprehensive and detailed dataset covering a wide range of attributes of seagrass dynamics, including dispersal, reproduction, and recovery from disturbance. *H. nigricaulis* is an ecosystem engineer in Port Phillip Bay where it occurs around the margins from the shallow subtidal zone to depths of 8 m. It provides ecosystem services, such as water filtration (Lee et al. 2012), carbon sequestration (Macreadie et al. 2014b), biological productivity for marine food webs (Warry et al. 2009), and nursery habitats for key recreational and commercial fish species (Jenkins et al. 2011; Smith et al. 2011).

The distribution of *H. nigricaulis* cover in the bay has been monitored for approximately 70 years. Over this period it has varied without any consistent pattern; some areas increased, others declined, and yet others fluctuated (Ball et al. 2014). The lack of any bay-wide pattern in seagrass cover made it difficult for coastal managers to pinpoint factors influencing seagrass cover and thus to manage seagrass effectively. Because Port Phillip Bay is such a large embayment covering >2000 km$^2$, there is large variation in physical (e.g. currents, circulation), chemical (e.g. nutrient inputs), biotic (e.g. herbivores), and anthropogenic processes (e.g. boating impacts) acting on seagrass populations across the bay.

For many years it was thought that changes in seagrass cover could be due to nutrient and sediment inputs (Bulthuis et al. 1992; Jenkins et al. 2015). Moderate levels of nutrients can positively affect seagrasses by improving productivity of nutrient-limited plants, but high levels can have negative impacts by increasing epiphyte loads, whereas sediments can reduce light availability and bury seagrasses (Burkholder et al. 2007). Some support for these theories is provided by a series of studies [including modeling, chemical analyses, and manipulative experiments; Jenkins et al. (2015)], showing that bay-wide patterns in seagrass distribution are driven by wave exposure (a proxy for sediment loading) and depth (a proxy for light availability for seagrass growth).

Jenkins et al. (2015) concluded that seagrass within the bay could be classified into three broad categories. First, there are seagrass populations growing in isolated pockets within the bay (e.g. Swan Bay and Corio Bay) that are sheltered from hydrodynamic stressors (currents and waves) and fluvial inputs (e.g. runoff) and have relatively stable cover. These 'persistent' populations grow in muddy soils where nutrients are derived from detrital inputs. Second, there are seagrass

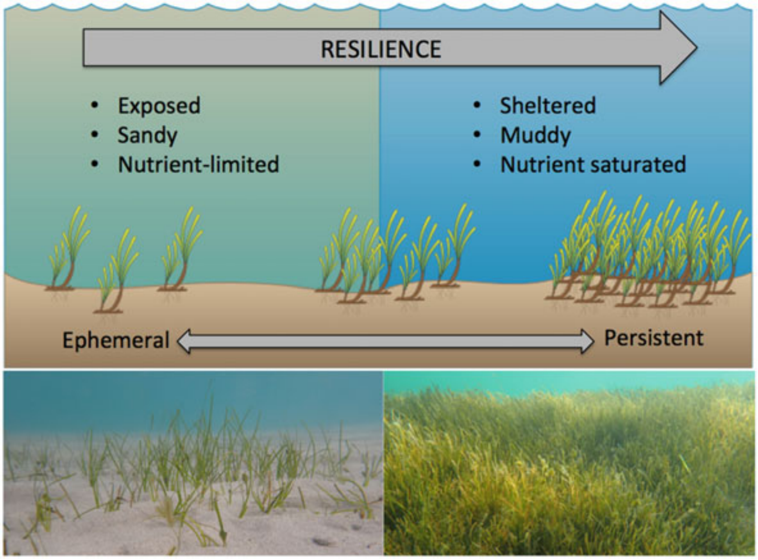

**Fig. 7.3** Dynamics of seagrass populations vary among locations for *Heterozostera nigricaulis* in Port Phillip Bay. Populations living in sandy, nutrient-limited environments are more ephemeral and have little tolerance to nutrient and sediment stress, whereas populations in muddy, nutrient-saturated environments appear less susceptible to nutrient and sediment stress and are therefore more persistent

populations living in exposed areas of the bay (e.g. Bellarine Peninsula and southern areas of the bay) that fluctuate in response to changes in fluvial inputs and sediment movement, and are considered ‘ephemeral’. Third, there are seagrass populations along the north-west coast of the bay that grow in fine sediments, are under regular turbidity stress, and respond positively to nutrients from a nearby sewage treatment plant (Hirst et al. 2016). Not surprisingly, differences in the population dynamics of seagrass in these three regions have implications for their resilience to changes in water quality in the form of nutrient and sediment stress. For example, the persistent populations are relatively unaffected by nutrient and sediment loading, whereas ephemeral populations respond rapidly to changes in catchment inputs and climate that affect nutrient and sediment supply (Fig. 7.3).

## 7.3 Evidence for Changes in Seagrass Cover Over Time

The important role of seagrass in the provision of ecosystem services has led to alarm at the perceived losses in seagrass cover in Australia and elsewhere. Much of the literature is focussed on major, sometimes rapid declines, and there are clear examples internationally of on-going, incremental losses of seagrass that reach a tipping point beyond which entire areas become devoid of seagrass (e.g. Cunha and

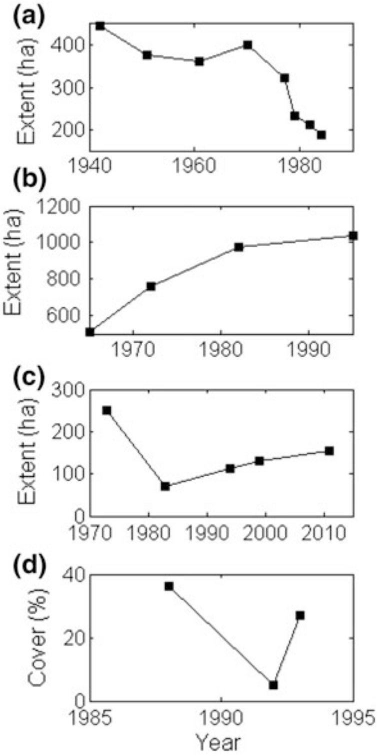

**Fig. 7.4** Examples of population dynamics of seagrass in Australia: **a** *Posidonia australis*, Southern Shore, Botany Bay, NSW (redrawn based on data from Larkum and West 1990); **b** *Posidonia coriacea*, *Amphibolis griffithii*, Success Bank, WA (redrawn from Kendrick et al. 2000); **c** *Heterozostera nigricaulis*, *Zostera muelleri*, Westernport, VIC (redrawn from Blake and Ball 2001; Kirkman 2014); **d** *Halophila* spp., Hervey Bay, QLD (redrawn from Preen et al. 1995)

Santos 2009; Fonseca and Bell 1998). Notwithstanding this emphasis on thresholds and non-linear changes, however, an analysis of the dynamics of seagrass in Australia shows that several different patterns of change occur, including: (1) massive losses over a decade, without recovery, after decades of stability (NSW, Fig. 7.4a), (2) steady, linear increase (WA, Fig. 7.4b), (3) massive losses over a decade, followed by partial recovery in subsequent decades (VIC, Fig. 7.4c), and (4) relatively quick loss, with full recovery (QLD) (Fig. 7.4d). These diverse examples highlight the need for robust monitoring of patterns in seagrass distributions, with finer spatial and temporal resolution, to support future efforts at understanding resilience.

## 7.4 Application of Resilience Theory to Australian Seagrass

Resilience is a popular concept in the management of natural resources in coastal waters because in many situations managers know what habitat is there and would prefer to retain it. The term is used frequently in relation to seagrass ecosystems because one of the most common changes observed for seagrass meadows is a shift to an unvegetated or an algal-dominated habitat, both of which are considered to provide fewer ecosystem services (Unsworth et al. 2015). Resilience is, formally, a specific property of complex systems, being the capacity of the system to retain structure and function in the face of disturbance. This capacity manifests through two potential avenues: resistance to change, and recovery after a temporary loss of structure and function (Folke et al. 2004).

Feedback loops play an important role in maintaining the structures and functions of ecosystems. External pressures e.g. pollution or climate change can reduce the strength of these feedbacks to the point where the ecosystem reaches a tipping point and there is a fundamental change in state (Nyström et al. 2012). The new state and its structure and function is then reinforced by a new set of feedbacks (unvegetated substrate, Fig. 7.5). The existence of the different sets of feedbacks in maintaining alternative states has important implications. First, ecosystems are vulnerable to rapid change at a particular level of disturbance—a tipping point—which can be difficult to predict. Second, due to the feedbacks that work to maintain the system in its new state, it can be challenging to return a system to its original state simply by removing the stressor. Hysteresis in the system can mean that

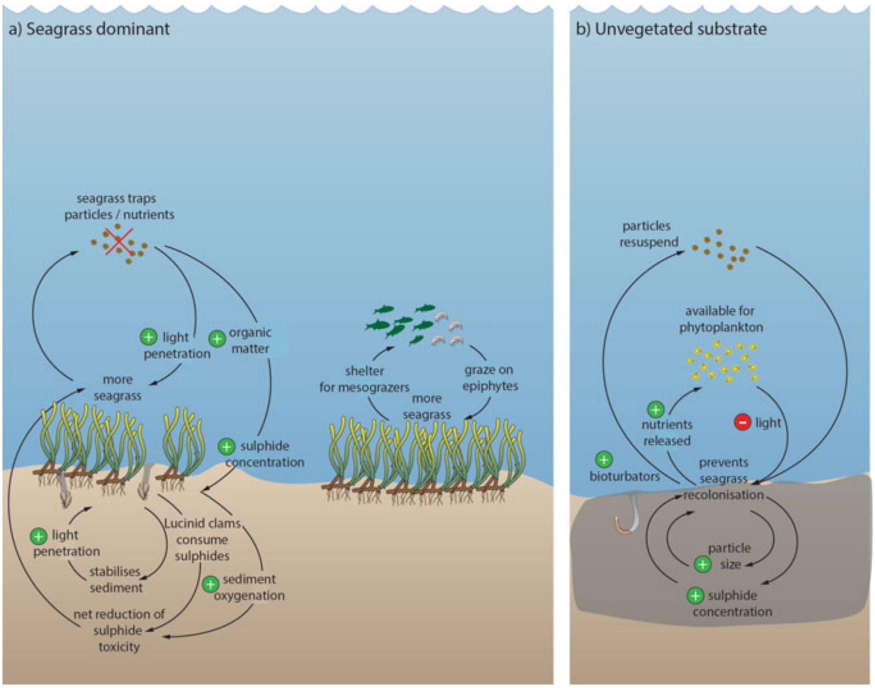

**Fig. 7.5** Examples of feedback loops in seagrass ecosystems that mitigate the relationship between changing levels of environmental stress (disturbance) and the response of seagrass, in: **a** seagrass dominant habitat, and **b** unvegetated substrate (from Maxwell et al. 2017)

recovery only occurs after the original stressor is reduced to a level well below that at which the tipping point occurred (Duarte et al. 2009).

We have recently begun to study feedback explicitly in seagrass systems in Australia as part of a global increase in understanding their importance (Unsworth et al. 2015). As ecosystem engineers, seagrasses provide obvious structure in what is often an otherwise unstructured, unvegetated system. They also modify the environmental conditions in the sediment and water column. The strong influence of seagrasses on their environment has led to overt recognition of the feedbacks that help maintain the health and persistence of seagrass meadows in Australia (Maxwell et al. 2015).

The concepts of non-linear changes and tipping points are prevalent in seagrass literature but, as we have shown above, patterns of change in seagrass cover vary widely. In many cases the low frequency of monitoring prevents a rigorous assessment being made of whether declines are linear or non-linear. We point out, therefore, that the principles of resilience, feedbacks and alternative states apply equally to scenarios where changes in the amount of habitat are linear or non-linear (Hughes et al. 2013). A resilience approach therefore has very widespread applicability in research supporting seagrass protection and conservation, regardless of the precise pattern of change in seagrass cover.

### 7.4.1 Feedbacks in Australian Seagrass Systems

The processes conferring resilience in seagrass have been examined for *Zostera muelleri* meadows in the subtropical waters of Moreton Bay, southern Queensland. Maxwell et al. (2014) measured the response of seagrass to disturbance from floodwaters entering the bay after the largest rainfall event in 40 years. Three key feedbacks bestowing a capacity for seagrass to resist decline during a pulse of extremely poor water quality were identified: (1) efficient removal of excessive nutrients from the water column leading to limited phytoplankton growth and improved water clarity, (2) increased deposition and suppressed resuspension of sediment and improved water clarity, and (3) provision of habitat for small grazing animals and thus more rapid removal of epiphytic algae (Maxwell et al. 2014). Although the strength of influence of specific feedbacks is dependent on location and the nature of the disturbance (Suykerbuyk et al. 2012), the key feedbacks in Moreton Bay meadows are consistent with those reported from studies elsewhere in the world (Fig. 7.5; Maxwell et al. 2017).

### 7.4.2 Alternative States

The concept of alternative states in seagrass ecosystems is also understood for the *Zostera muelleri* meadows of Moreton Bay (Maxwell et al. 2015). First, the physiological and morphological responses of seagrass to changing water quality are known; second, the role of key feedbacks in seagrass persistence has been quantified; and third, current and historical distributions of seagrass are mapped. These three aspects were combined in a Bayesian Belief Network model and used to predict seagrass presence and absence: a comparison between predicted, actual and historical distributions demonstrated true alternative states. That is, at certain, intermediate levels of water quality, if seagrass is present it persists, but if it is absent it cannot re-establish (Maxwell et al. 2015). Such areas have now been mapped and henceforth provide a focus for coastal resource managers (Gilby et al. 2016; Henderson et al. 2017).

### *7.4.3 Measuring Resilience*

Resilience is a property of complex, adaptive systems that is driven by multiple feedbacks and interactions between biotic and abiotic components across a range of spatial and temporal scales (Gunderson 2000). This complexity can make it difficult to predict ecosystem responses to stressors. Traditional measures used to assess the state of seagrass ecosystems, such as seagrass density, cover, biomass and extent, are not good proxies for resilience because they can remain at high levels even as the system is close to collapse (e.g. Soissons et al. 2014).

The focus of much of the research into the resilience of Australian seagrass meadows has been on recovery rates, and the mechanisms by which seagrass cover at a particular location returns to a previous amount. Such studies provide valuable information on the potential of species to recover from disturbance on a small scale; for example, re-establishment of *Halophila ovalis* in a Western Australian estuary following multiple disturbances (Eklöf et al. 2010), and of *Heterozostera nigricaulis* in Port Phillip Bay, Victoria, following experimental removal of seagrass (Macreadie et al. 2014a). Recovery of seagrass at larger scales is more problematic, as it is for other coastal ecosystems, because a return to precisely the original state is less likely (Duarte et al. 2014). Quantifying recovery at the whole-of-system scale typically requires both a comprehensive dataset of seagrass responses to past disturbances and a capacity for dynamic modelling, to predict critical thresholds where the balance can shift from recovery to decline (Standish et al. 2014). It is also important to note that in the dynamic, open type of system applicable to most seagrass ecosystems, resilience needs to be defined and measured within the bounds of a specific period and for particular environmental conditions (Standish et al. 2014).

### *7.4.4 Managing for Resilience*

The concept of managing stressors on environmental systems to maximise system resilience is both popular and worthwhile (Walker and Salt 2012). For seagrass, the steps required to manage for resilience are similar to, but not necessarily the same as, those traditionally used to protect or conserve seagrasses. Where the understanding of resilience allows it, the emphasis should be on managing to enhance key feedback processes (Maxwell et al. 2015). In the absence of comprehensive datasets and an understanding of resilience of seagrass at a particular location, a generic strategy of protecting features likely to be important in resilience is recommended. Unsworth et al. (2015) list ten actions that have been used successfully to enhance resilience of seagrasses internationally (Table 7.1). To manage a system for resilience we should aim to preserve as many of the underlying traits as possible.

Addressing the capacity of the ecosystem to promote natural seagrass recovery is also important for enhancing the recovery potential of seagrass meadows. The role of dispersal of genetic material in connectivity among meadows is a particularly important component of the capacity for recovery (Kendrick et al. 2012). The sources of genetic material are often a function of the species present and prevailing hydrological conditions (Kendrick et al. 2012), with seeds of some species travelling up to 400 km and of others just a few metres.

## 7.5 Conclusions

The scientific study of the resilience of Australian seagrasses is advancing rapidly, assisted by an improved theoretical framework for resilience research on seagrass and other coastal habitats. This improved understanding is having far-reaching implications for expectations of how seagrasses should be monitored and managed. While the long-standing reporting of seagrass dynamics in many locations in Australia has been helpful, it is clear that changes in seagrass extent and biomass need monitoring at finer temporal and spatial resolutions than has often been the case historically. There is now a much clearer focus on understanding and monitoring characteristics of seagrasses and their environment to inform management aimed at enhancing the resilience of seagrass ecosystems.

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# Chapter 8
# Reproductive, Dispersal and Recruitment Strategies in Australian Seagrasses

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**Abstract** Seagrasses are a relatively small group of marine angiosperms that have successfully colonised the oceans and includes monecious, dioecious and hermaphroditic species. They display a range of mating systems, dispersal mechanisms and recruitment strategies that have allowed them to adapt and survive within the marine environment. This includes a general reduction in the size and complexity of floral structures, and subsurface pollination (hydrophily) in the majority of species.

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Fertilisation occurs through water-dispersed pollen that is typically filamentous and sticky, however, recent work has also suggested that marine invertebrates may play a role in pollen movement and fertilisation. Seed size and morphology varies widely among species, from fleshy floating fruit (e.g. *Posidonia*) to small negatively buoyant seeds less than 0.5 mm (e.g. *Halophila*). Nearly all species retain some capacity of asexual reproduction through rhizome elongation or the production of asexual fragment or propagules that can be more widely dispersed. These differences in reproductive strategies have important effects on recruitment and dispersal potential and subsequent population dynamics. Direct estimates of dispersal and recruitment are inherently difficult to assess in seagrasses, but the use of novel genetic and predictive modelling approaches are providing new insights into these important processes. This chapter highlights the main reproductive strategies and adaptations seagrass have undergone in response to reproducing in a marine environment, with an emphasis on Australian seagrass species. We highlight the current state of knowledge in Australian seagrass reproductive biology and future directions in seagrass reproductive biology research.

## 8.1 Introduction

Seagrasses are marine angiosperm and the only true flowering plants to have successfully colonised the marine environment from freshwater ancestors (den Hartog 1970; Du and Wang 2014; Les et al. 1997; Philbrick and Les 1996; Sculthorpe 1967). They are a relatively small polyphyletic group of monocotyledons comprised of six plant families; the Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Ruppiaceae, Zannichelliaceae and Zosteraceae. In total there are only around 72 species (Short et al. 2011), although there is still considerable debate surrounding the taxonomic status of several groups (Coyer et al. 2013; Jacobs et al. 2006; Kuo 2005; Kuo and den Hartog 2006; Les et al. 1997, 2002). Seagrasses display a range of mating systems, dispersal mechanisms and recruitment strategies that have allowed them to adapt and survive within the marine environment. While most species have retained the capacity for both sexual and asexual reproduction, seagrasses show relatively low levels of diversity in reproductive morphology compared to terrestrial angiosperms, likely resulting from convergent evolution and constraints imposed by reproducing within the marine environment.

The majority of seagrass species (90%) produce unisexual or imperfect flowers that lack either male or female reproductive organs, with the Posidoniaceae being the only family to produce true bisexual or hermaphroditic flowers (Ackerman 2006; Les 1988; Les et al. 1997). Of those species that exhibit unisexual flowers, over 60% are dioecious (flowers are produced on separate plants), and less than 40% are monecious (flowers are produced on different parts of the same plant) (Les 1988; Les et al. 1997). While many freshwater aquatic species have retained aerial flowers and pollination, seagrasses display some of the most extreme adaptations to fertilization in an aquatic environment, with all except one species (*Enhalus*

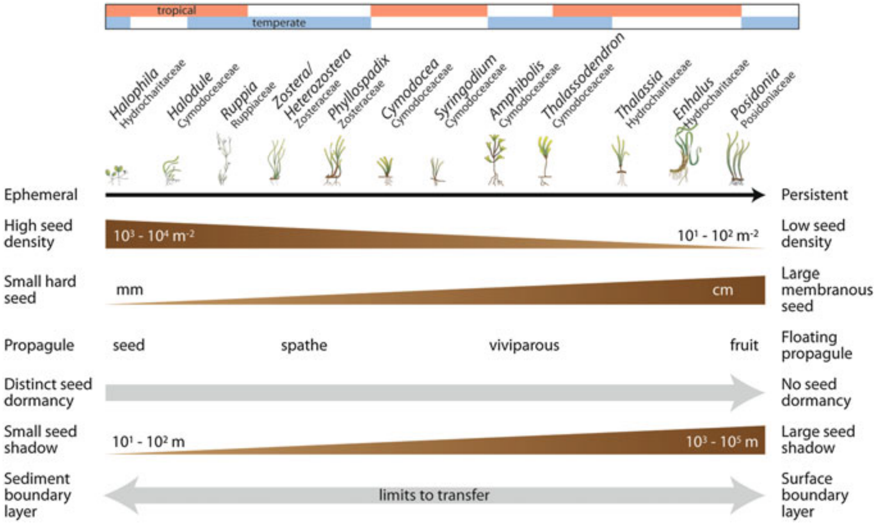

**Fig. 8.1** Reproductive characteristics of tropical and temperate seagrasses, including reproductive effort, reproductive structures, and hydrodynamic interface driving seed or propagule dispersal. Abbreviations: m meters; m$^{-2}$ per square meter; cm centimeters (From Kendrick et al. 2012)

*acoroides*) showing subsurface pollination (hydrophily) (Ackerman 1995; Cox 1988; Les 1988). The transition to hydrophily has resulted in reduced floral organisation of submerged flowers and inflorescences, and the production of sticky filamentous pollen that facilitates movement in the marine environment and capture by female reproductive structures (Ackerman 1995, 2006).

Seeds represent an important dispersal mechanism for seagrass species, and seed characteristics and germination strategies vary widely (den Hartog 1970; Inglis 2000b; Kendrick et al. 2012; Kuo and Kirkman 1996; Orth et al. 2000, 2006). The general reproductive characteristics of tropical and temperate Australian seagrasses, including reproductive effort, reproductive structures, and hydrodynamic interface driving seed or propagule dispersal are given in Fig. 8.1 and Table 8.1. Seeds can vary in size from less than a millimetre in some *Halophila* species, to more than 1 cm in *E. acoroides* (Orth et al. 2006). Some species produce positively buoyant seeds or fruit that have the capacity for long distance dispersal (e.g. *Enhalus*, *Thalassia* and *Posidonia*), while others produce negatively buoyant seeds with limited dispersal potential (e.g. *Zostera* and *Halophila*) (Kendrick et al. 2012; Lacap et al. 2002). Nevertheless, dispersal of these seeds over large distances may still occur via transport of detached fragments carrying spathes (e.g. *Zostera* species, Harwell and Orth 2002). The seeds of some species lack any dormancy period or seed bank (e.g. *Amphibolis* and *Posidonia*), while others can remain dormant for long periods of times, although the germination cues for most species remain poorly understood (Inglis 2000b; Orth et al. 2000, 2006).

While sexual reproduction is clearly important in maintaining seagrass populations, most species also use various forms of clonal propagation (Kendrick et al. 2017). Asexual reproduction in seagrasses can occur via localised rhizome extension, and

**Table 8.1** Reproductive characteristics of from different seagrass genera

| Species | Dicliny | Flower location | Pollen type | Fruit characteristics | Seed characteristics | Reference |
|---|---|---|---|---|---|---|
| **Zosteraceae** | | | | | | |
| *Heterozostera* spp. | Monoecious | Inflorescence (Spathe) among leaves | Filiform | Spathe on shoot (11–23 mm) | Dormant (1.4–3.5 mm) | Kuo (2005) |
| *Zostera marina* | Monoecious | Inflorescence (Spathe) among leaves | Filiform (2700 × 7.5 μm) | Spathe on shoot | Dormant (3.1–3.8 mm); Sv = 5.96 cm $s^{-1}$; specific gravity 1.13 ± 0.03 | Willie-Echeverria et al. (2003), Orth et al. (1994), Hosokawa et al. (2015) |
| *Phyllospadix* spp. | Dioecious | Inflorescence (Spathe) among leaves | Filiform (1500 μm) forming clumps of ~2 mm | Spathe on shoot | Dormant | Reed et al. (2009) |
| **Cymodoceae** | | | | | | |
| *Amphibolis* spp. | Dioecious | Short shoot | Filiform (3–5000 × 20 μm) | – | Viviparous seedling attached to mother from 7 to 12 months | Kuo et al. (1990) |
| *Cymodocea rotundata*, *Cymodocea serrulata* | Dioecious | Basal leafs | Filiform (2000 × 10 μm) | | Dormant seeds attached to rhizome (5–10 mm) | Waycott et al. (2004) |
| *Halodule uninervis* | Dioecious | Basal leafs | Filiform (1000 μm) | Attached to rhizome | Dormant (~2 mm) | Waycott et al. (2004) |
| *Halodule wrightii* | | | | | (2.1 ± 0.1 mm) | Darnell et al. (2015) |
| *Syringodium isoetifolium* | Dioecious | Inflorescence | Filiform | Floats | Dormant (4–8 mm) | Waycott et al. (2004) |

(continued)

**Table 8.1** (continued)

| Species | Dicliny | Flower location | Pollen type | Fruit characteristics | Seed characteristics | Reference |
|---|---|---|---|---|---|---|
| *Thalassodendron ciliatum* | Dioecious | Canopy | Filiform (5000 × 20 μm) | – | Viviparous seedling | Waycott et al. (2004) |
| **Posidoniaceae** | | | | | | |
| *Posidonia* | Bisexual | Inflorescence | Filiform (500–1000 μm) | Positively buoyant, ellipsoidal | Not dormant | |
| *Posidonia australis* | | | | 24.5 ± 0.33 mm | (21.2 ± 0.34 mm)<br>Sv = 10.6 ± 0.38 cm $s^{-1}$ | Ruiz-Montoya et al. (2012) |
| *Posidonia coriacea* | | | | | Sv = 17.1 ± 2.34 cm $s^{-1}$ | Orth (1999) |
| **Hydrocharitaceae** | | | | | | |
| *Enhalus acoroides* | Dioecious | Female flower is raised to the surface for pollination | Spherical (150–175 μm diameter) | Ovoidal | Not dormant ()<br>Sv = 10.0 ± 0.1 cm $s^{-1}$ | Lacap et al. (2002) |
| *Halophila beccarii* | Monoecious and dioecious | Basal leafs | Ellipsoidal (80 × 40 μm) | Spherical | Spherical dormant | Parthasarathy et al. (1988) |
| *Halophila ovalis* | | | | Spherical<br>(3 ± 0.15 mm)<br>Sv = 5.4 ± 0.26 cm $s^{-1}$ | Spherical<br>(1.29 ± 0.03 mm)<br>Sv = 4.7 ± 0.14 cm $s^{-1}$ | Ruiz-Montoya et al. (2012) |
| *Thalassia hemprichii* | Dioecious | Basal shoot | Spherical (80–100 μm) | Positively buoyant, spherical | Not dormant<br>Sv = 10.0 ± 0.2 $cm^{-1}$ | Lacap et al. (2002) |
| *Thalassia testudinum* | | | | | (15.1 ± 0.8 mm) | Darnell et al. (2015) |

Adapted from Orth et al. (2006) and Ackerman (2006). In parenthesis are dimensions, Sv. refers to settling velocity through the production of vegetative propagules (e.g. rhizome fragments, pseudoviviparous plantlets) (Ballesteros et al. 2005; Cambridge et al. 1983; Kuo et al. 1987; Sinclair et al. 2016b; Thomson et al. 2015). There has been much debate regarding the ecological and evolutionary consequences and benefits of the two modes of reproduction (Ehlers et al. 2008; Massa et al. 2013; Pan and Price 2001; Reusch et al. 2005; Silvertown 2008), however, it is clear from the increasing number of molecular studies that the relative importance of sexual versus asexual reproduction for meadow maintenance varies widely within, and among species (Alberto et al. 2005; e.g. Billingham et al. 2003; Evans et al. 2014; Reusch and Bostrom 2011; Sherman et al. 2016).

Seagrasses clearly display a wide variety of reproductive and mating strategies, while at the same time being constrained by fertilization in the marine environment. The aim of this chapter is to highlight the main reproductive strategies and adaptations seagrass have undergone in response to reproducing in a marine environment, with an emphasis on Australian seagrass species. We highlight the current state of knowledge in Australian seagrass reproductive biology and future directions in seagrass reproductive biology research.

## 8.2 Diversity of Flowering Strategies, Flowers, Pollination and Seed Production

The recolonization of marine environments by flowering plants has occurred on at least three separate occasions and resulted in a diversity of reproductive strategies within the functional group we know today as seagrasses (Cook 1999; Les et al. 1997) (Table 8.1). However, challenges faced by angiosperms in their transition from terrestrial to marine environments, such as the need for pollination to occur in an aqueous environment, has led to the convergence of a number of seagrass reproductive characters (Ackerman 2006). One such trait is the development of unisexual flowers with a high degree of dioecy; the presence of male and female flowers on separate plants (see Table 8.1). All Australian genera from the families Cymodoceaceae (*Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium* and *Thalassodendron*), as well as the genera *Enhalus*, *Thalassia* and some *Halophila* species within the family Hydrocharitaceae, are dioecious (Ackerman 2006). Within the genus *Halophila* the majority of Australian species are dioecious including *H. ovalis*, *H. spinulosa*, *H. ovata*, *H. tricostata*, and *H. australis*, while *H. decipiens* and *H. capricorni* both have unisexual flowers on monoecious plants (Kuo and Den Hartog 2001). The other dioecious genus is *Phyllospadix* (family Zosteraceae), but it does not occur in Australia. Within the family Posidoniaceae, species are monoecious with bisexual flowers, while the remaining Australian Zosteraceae (*Heterozostera nigricaulis* (syn. *Zostera nigricaulis*; for the current status of *Heterozostera* see the Appendix) and *Zostera muelleri*) are monoecious with diclinous (unisexual) flowers.

One potential advantage of dioecy or unisexual flowers in monoecious plants is to reduce the occurrence of self-pollination and inbreeding and to promote outcrossing (Kendrick et al. 2012), however it may also be a relic of ancestral conditions and thus an evolutionary constraint (Les 1988). This is because diclinous flowering monoecious plants can overcome geitonogamy or selfing (the pollination of a flower by pollen from another flower from the same plant) by staggering the development of male and female flowers parts known as dichagomy. For example, in *Posidonia*, selfing is avoided within individual flowers by protandry where the stigmas only become receptive after pollen is released (McConchie and Knox 1989). *Zostera* species, on the other hand, display protogyny where male flowers will only open after female flowers have lost their styles (Reusch 2003; Zipperle et al. 2010). In both these cases, geitonogamy (pollination) is possible among separate flowers of the same clone resulting in a mixed mating system where both selfing and outcrossing exist (Reusch 2003; Sinclair et al. 2014b; Zipperle et al. 2010).

Hydrophily, the pollination of a flower in an aqueous environment is a common feature of seagrass plants. All species with the exception of *E. acoroides* undergo subsurface pollination. In *E. acoroides* pollination occurs on the water surface, which typically limits them to shallow intertidal or subtidal habitats, although they can occur in deeper water where recruitment from vegetative propagules may play an important role (Vermaat et al. 2004). Pollen in this species is spherical and buoyant and is released from submerged males flowers, or is transported to the surface by detached buoyant male flowers. Once at the surface the pollen encounters the female inflorescence that is attached to a long peduncle (Ackerman 2006; Tanaka et al. 2004; Vermaat et al. 2004). In all other seagrass species, adaptations in morphology and other features of pollen have occurred to aid subsurface pollination. The evolution of filiform, or thread-shaped pollen in all genera of the Posidoniaceae, Cymodoceaceae and Zosteraceae families aids in the subsurface dispersal of pollen via water currents, and in the capture of the pollen by female flowers (Ackerman 1995, 2006). Of the remaining two genera in the Hydrocharitaceae family, *Thalassia* has spherical pollen, however, these are transported in long filamentous chains held together by mucilaginous material, and *Halophila* has ellipsoid shaped pollen which are transported four at a time within a filamentous structure (Ackerman 2006). Seagrass pollen has converged in other features that promote subsurface pollen dispersal and pollination such as neutrally buoyant pollen that is often covered in a sticky gelatinous fluid allowing attachment to female flowers, and the production of large amounts of pollen (Sinclair et al. 2014b).

While dispersal of pollen via water currents has been regarded as the main mode of pollination in seagrasses, recent experimental evidence has suggested a role for invertebrate fauna in transporting pollen embedded in mucilage mass from male flowers to the stigma of female flowers in the tropical seagrass *Thalassia testudinum* (van Tussenbroek et al. 2016). This newly discovered phenomenon might occur more commonly in seagrass pollination than previously realised and warrants further investigation in other species.

### 8.2.1 Reproductive Structures

The flowers of seagrasses are generally reduced and unremarkable in appearance due to their underwater reproduction negating the need to attract animal pollinators (Ackerman 2006). A summary of the major characteristics of seagrass reproductive structures can be found in Table 8.1. Flowers in the Zosteraceae family develop enclosed in leaf-like structures known as spathes on reproductive shoots among the leaf canopy (Kuo 2005) (Fig. 8.2). In some species, such as *Zostera marina*, spathes occur grouped on branching shoots called rhipidia (Hosokawa et al. 2015). Zosteraceae seeds mature within the spathe and develop into an ellipsoid shape with a hard seed coat (Waycott et al. 2004) (Fig. 8.3). Seed size can vary significantly within species depending on the environmental conditions experienced by the parent plant (Wyllie-Echeverria et al. 2003). Seeds are negatively buoyant and generally settle quickly after release, however, if the rhipidia or spathes are released from the parent plant they may remain positively buoyant for several weeks, aiding in long distance dispersal (Källström et al. 2008). Seeds can accumulate in the sediment, forming a dormant seed bank reaching densities of tens of thousands per

**Fig. 8.2** Spathes growing on reproductive shoots of *Heterozostera nigricaulis*. Spathes are the enclosed in leaf-like structures containing the flowers and developing seeds. Image courtesy of Leonardo Ruiz Montoya

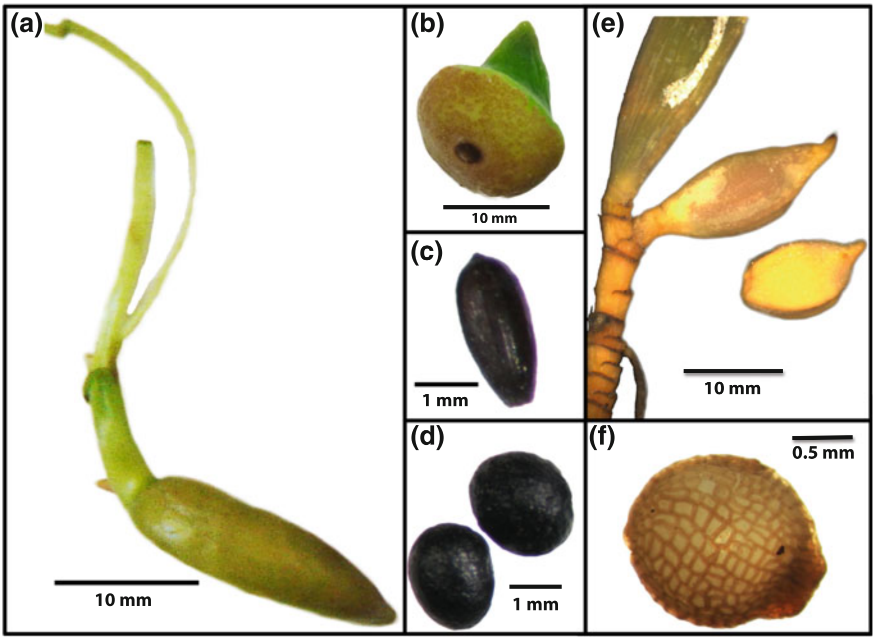

**Fig. 8.3** Seeds from Australian seagrasses. **a** Direct developing seed as released by fruit from *Posidonia australis*; **b** *Enhalus acoroides* seeds; **c** *Heterozostera nigricaulis* seed; **d** *Halodule uninervis* seed; **e** *Cymodocea serrulata* seed pod; **f** *Halophila ovalis* seed. Images courtesy of James Cook University, Leonardo Ruiz Montoya and Timothy Smith

square metre in some populations (Conacher et al. 1994a; Jenkins et al. 2015) (Fig. 8.1).

Within the Cymodoceaceae family, there is a more diverse array of flowering structures. *Cymodocea* and *Halodule* species have flowers at the base of the leaves and in the leaf sheath. *Cymodocea rotundata* and *C. serrulata* produce seeds that are attached to a rhizome (Fig. 8.3), while *Halodule uninervis* seeds usually develop within the sediment and, therefore, have limited dispersal (Waycott et al. 2004). Seed banks of *H. uninervis* can vary greatly spatially, reaching densities of 80,000 seeds $m^2$ in some populations (Inglis 2000b). *Syringodium isoetifolium* has simple flowers arranged in an inflorescence (cyme) among the leaves of the plant (Waycott et al. 2004). Seeds develop into a hard nut and mature on the inflorescence, which can be positively buoyant and act as a diaspore if detached from the plant before the seeds are released (Waycott et al. 2004). The remaining two genera in this family, *Amphibolis* and *Thalassodendron*, are the only seagrasses that produce viviparous seedlings on the mother plant (Kuo and Kirkman 1990). *Amphibolis antarctica* and *A. griffithii* have inconspicuous flowers occurring on the lateral stems of the seagrass. After fertilisation occurs the seedling forms on the parent plant for seven to twelve months, developing stiff bristles that form four combs that act as an anchor after detachment to secure the plant to the substrate

(Kuo and Kirkman 1990; Rivers et al. 2011). Roots emerge from the seedling after detachment (Kuo and Kirkman 1990). In *Thalassodendron ciliatum* and *T. pachyrhizum*, viviparous seedlings can remain attached to parent plants for months (until at least 3 cm in length) with the bract from the flower swelling to form a buoyant structure to aid dispersal (Waycott et al. 2004, 2014).

Seagrasses in the family Posidoniaceae contain hermaphroditic flowers borne in spiked inflorescences on stalks positioned within or above the canopy (Waycott et al. 2014). The fruit, a green drupe is positively buoyant which aids dispersal and contains a single negatively buoyant seed that has no dormancy (Ruiz-Montoya et al. 2012) (Fig. 8.3). Pseudovivipary, the formation of clonal plantlets has also been recently described in the Australian species *Posidonia australis* (Sinclair et al. 2016b) as well as the Mediterranean *P. oceanica* (Ballesteros et al. 2005) (see section on clonal reproduction and vegetative propagules below).

Flowers in the Hydrocharitaceae family vary greatly among genera. *Enhalus acoroides* has separate male and female flowers on long wiry stems. Male flowers are white and spheroid and released from the inflorescence onto the surface of the water where they may float for several km (Lacap et al. 2002). After pollination of the female flower, a large spiky fruit develops containing several seeds that germinate on release (Waycott et al. 2004). The dislodged fruit are positively buoyant and have a median dispersal distance of 41 km, while seeds, which are also positively buoyant, are limited to dispersal distances of around 5 km (Lacap et al. 2002) (Fig. 8.3). *Thalassia* species have flowers emerging from basal shoots with a long pedicel and separate into 6–9 parts with the ovary at the base of the female flower (Waycott et al. 2004). The fruit develops from the ovary at the base of the female flower into a dome-shaped capsule (Kuo et al. 1991) that is positively buoyant and has a median dispersal range estimated at around 23 km (Lacap et al. 2002). The pyriform seeds that are then released from the fruits may also maintain some positive buoyancy, extending dispersal by up to another 13 km (Lacap et al. 2002). *Halophila* species produce numerous small green fruits that each release small (~0.5 mm diameter) dormant seeds with a hard seed coat (Fig. 8.3). The number of seeds per fruit is highly variable among species (e.g., averaging 7 for *H. ovalis* and 30 for *H. decipiens*) (Kuo and Kirkman 1992; Waycott et al. 2004). The seeds are negatively buoyant and settle quickly with secondary dispersal limited to very energetic events such as storms (Ruiz-Montoya et al. 2012).

### *8.2.2 Reproductive Effort and Flowering Stimuli*

Reproductive effort (flower and seed production) is known to vary greatly within and among species, both spatially and temporally (Marbà and Walker 1999) with the mechanisms or stimuli driving this variation poorly understood. As with plants in general, seagrasses have been shown to allocate resources to flowering when under stress from disturbance. A review of reproductive effort in seagrasses found a general four-fold increase in flowering after disturbance, and this increased to

13-fold when the disturbance was anthropogenic in origin (Cabaço and Santos 2012). In *E. acoroides*, seagrass abundance was found to influence reproductive output with a threshold response resulting in a sharp increase in floral production when areal cover exceeded 50% (Vermaat et al. 2004). Flowering production in *Enhalus* has also been correlated with temperature and light levels (Rollon et al. 2003). Flower production in Australian Zosteraceae species can vary greatly both inter-annually and from site to site (Campey et al. 2002; Conacher et al. 1994b; Inglis and Lincoln Smith 1998; Smith et al. 2016b) ranging in densities from zero, to in excess of 3000 spathes per square metre for some species (e.g. *H. nigricaulis*, Smith et al. 2016b). While flowering in Australian Zosteraceae generally occurs in the austral spring and summer months, environmental cues for reproduction are not well studied. However, reproductive effort of *Z. muelleri* (syn. *Z. novazelandica*) in New Zealand, increased at extremes of high and low light (30 and 300 µE $m^{-2}$ $s^{-1}$ compared to 100 µE $m^{-2}$ $s^{-1}$), low salinity (17 psu produced 1.5 more flowers compared to 33 psu) and low temperature (with a threefold increase of flowering in plants cultured at 5 °C compared to those at 15 °C, while no flowering occurred at 25 °C) and areas of high seagrass biomass (Dos Santos and Matheson 2017; Ramage and Schiel 1998). Flowering in *Posidonia* species in Australia is also highly variable and thought to be influenced by temperature, with the onset of flowering beginning in mid-winter (Inglis and Lincoln Smith 1998; Kendrick et al. 2012; Smith and Walker 2002). Flowering intensity in *P. oceanica* in the Mediterranean has been shown to increase greatly after hot summers (Diaz-Almela et al. 2006). Experimental culture of seagrasses in tanks also indicates that temperature plays a role in the onset of flowering in tropical seagrass species including *C. serrulata*, *S. isoetifolium*, and *Thalassia hemprichii*, which commonly occur in Australian meadows (McMillan 1980).

## 8.3 Clonal Reproduction and Vegetative Propagules

All seagrasses reproduce asexually and this mode of reproduction has long been recognised to play an important role in the establishment and growth of seagrass populations (Grace 1993; Li 2014; Philbrick and Les 1996; Sculthorpe 1967). Asexual reproduction in seagrasses can occur via several different mechanisms; these include: (1) localised rhizome extension (Fig. 8.4a), (2) detachment of rhizome/shoot fragments (Fig. 8.4b), (3) production of specialised vegetative propagules (Fig. 8.4c) and (4) pseudovivipary where the floral organs are replaced by asexually produced plantlets (Cambridge et al. 1983; Kendrick et al. 2012; Kuo et al. 1987; Sinclair et al. 2016b; Thomson et al. 2015). While rhizome extension within seagrass beds has long been recognised as important for population maintenance and bed architecture, the role of vegetative propagules (e.g. rhizome fragments, vegetative aerial shoots) in maintaining local populations, and contributing to long distance dispersal has only recently being realised (Kendrick et al. 2012; McMahon et al. 2014; Sherman et al. 2016; Stafford-Bell et al. 2015;

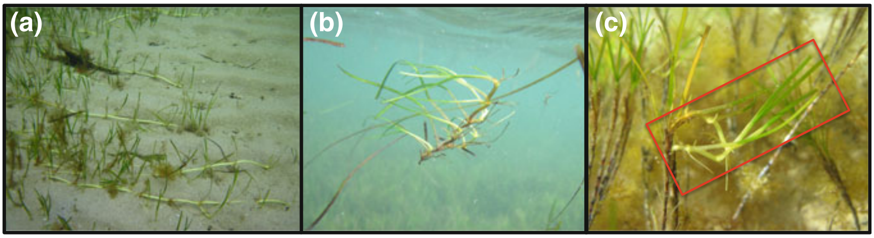

**Fig. 8.4** Examples of asexual reproduction in Australia seagrasses. **a** Localised rhizome extension of a *Zostera muelleri* bed; **b** detachment of rhizome/shoot fragments of *Zostera muelleri*; **c** production of specialised vegetative propagules (insert) of *Heterozostera nigricaulis*

Thomson et al. 2015). This is because the increase in the number of molecular studies now allows for the direct identification of putative clones that may have dispersed within and between populations. Additionally, vegetative fragments also have the potential to carry and disperse seeds over long distances, further contributing to gene flow and enhancing genetic diversity (Erftemeijer et al. 2008; Källström et al. 2008).

### *8.3.1 Rhizome Elongation and Clonal Patch Size*

Seagrass species have a rhizome system that allows for the horizontal expansion of plants under the sediment surface and is the main mechanism for clonal reproduction and growth. The basic iterative unit of seagrass is the ramet, which consists of a portion of rhizome with associated roots, and leaf bearing shoots that grow from the rhizome structure. As the rhizome extends under the sediment it branches and can become detached, forming multiple modular units (ramets) that are physiologically independent but have the same genotype (genet). The rate of elongation of the rhizome and the branching pattern (frequency and angle of branching) therefore determines the basic pattern of clonal growth and is highly variable between species (Kendrick et al. 2005). The extent and rate of rhizome extension (and therefore the clonal patch size within a meadow) also shows considerable spatial and temporal variation within species, in response to local abiotic (e.g. nutrient availability, sediment inundation and water movement), and biotic (e.g. plant shoot density and grazing intensity conditions) (Jensen and Bell 2001; Kendrick et al. 2005; Marbà and Duarte 1994, 1998; Marbà and Walker 1999; Perez et al. 1994). Empirical and modelling studies of several species have shown non-linearity in the interactions between ramets as they grow, such that the growth rate of seagrass patches accelerates as they increase in size (Kendrick et al. 1999, 2005; Marbà and Duarte 1998; Sintes et al. 2005; Vidondo et al. 1997). Rhizome growth rates have only been determined for a limited number of Australian seagrass species (Campbell and McKenzie 2004; Marbà and Duarte 1998; Marbà and

Walker 1999; Meehan and West 2000; Turner 2007). Species belonging to the genera *Amphibolis*, *Posidonia* and *Thalassodendron* all show relatively slow rhizome elongation rates (1–35 cm per year), while *Zostera* species tend to have much faster rhizome elongation rates (25–150 cm per year) (Campbell and McKenzie 2004; Marbà and Duarte 1998; Marbà and Walker 1999; Meehan and West 2004; Turner 2007). Information on the patch size of clones and the fine-scale spatial distribution of genotypes within meadows remains largely unknown for most species. However, these factors are likely to have a number of important mating system consequences in seagrass meadows. For example, in monecious species, such as those in the genus *Zostera*, and hermaphrodidtic species in the genus *Posidonia*, the opportunity for outcrossing will be limited when clones dominate large areas (mate limitation). Pollen typically has limited dispersal capacity and therefore in populations with large clonal patches, pollen may encounter the reproductive organs of the same genetic individual resulting in self-fertilisation. Self-fertilisation is the most extreme form of inbreeding and can lead to a loss of fitness (although if selfing occurs extensively over long periods this can lead to a purging of deleterious recessive alleles and increase in fitness) (Charlesworth and Wright 2001). The degree of intermingling of genotypes and the level of genotypic diversity at fine spatial scales has been shown to play an important role in maintain a range of ecosystem functions. For example, several studies in *Z. marina* have shown that levels of genotypic diversity plays an important role in determining resilience to disturbance (Hughes and Stachowicz 2004, 2011; Massa et al. 2013), levels of productivity and faunal diversity (Reusch et al. 2005), increases restoration success (Reynolds et al. 2012, 2013) and the ability of seagrass meadows to cope with the effects of climate change (Ehlers et al. 2008; Reusch et al. 2005).

### *8.3.2 Vegetative Fragments*

The dispersal and recruitment of seagrass fragments was previously thought to be rare (Ewanchuk and Williams 1996), however, there is increasing evidence that the importance of these fragments to population maintenance has been underestimated (Di Carlo et al. 2005; Hall et al. 2006; Kendrick et al. 2005; Thomson et al. 2015). Most seagrass species are prone to fragmentation due to the action of wind, waves, ocean currents, herbivory and various anthropogenic disturbances (e.g. dredging, boating and aquaculture activities) (Erftemeijer and Lewis III 2006; Li 2014; Sculthorpe 1967; Thomson et al. 2015). Different types of fragments can result from disturbance, however only some of these have the capacity to act as vegetative propagules. Fragments consisting of just the leaf shoots, with no associated rhizome or roots, are unlikely to establish as viable independent plants, but may contribute to long distance dispersal of seeds attached to the fragments [referred to as reproductive fragments which contain spathes, fruits and seeds—(Erftemeijer et al. 2008; Hall et al. 2006; Harwell and Orth 2002; Källström et al. 2008)].

Uprooted fragments consisting of rhizome, roots and shoots have the potential to act as vegetative propagules (Fig. 8.4b), although the viability and recruitment success of these vegetative fragments are only known for a limited number of species. Estimates of the period of viability of floating vegetative fragments varies widely between species, with some species potentially remain viable and actively growing for several weeks in the water column (e.g. *Z. muelleri* (Stafford-Bell et al. 2015), *Zostera noltii* (Berković et al. 2014), to just 1–2 weeks for *Halodule wrightii* and *Halophila johnsonii* (Hall et al. 2006). A study by Ewanchuk and Williams (1996) showed that the viability of vegetative fragments of *Z. marina* significantly declines after 6 weeks and that growth and re-establishment success of fragments declines with the amount of time spent in the water column. Survival of transplanted fragments of *Z. marina* is typically low with only 4–6% of transplanted fragments surviving to 12 weeks (Ewanchuk and Williams 1996). Natural recruitment of *P. oceanica* has been observed on rubble mounds from dump barges (Di Carlo et al. 2005), and natural vegetative fragment recruitment has also been reported for *P. australis* and *P. coriacea* in Western Australia, with 88 vegetative fragment recruits ha$^{-1}$ per year for *P. australis* and 18 vegetative fragments ha$^{-1}$ per year for *P. coriacea* (Campbell 2003). Of these, 31% of *P. australis* recruits showed rhizome growth and extension over a 23 month period, but no rhizome growth was observed for *P. coriacea* recruits (Campbell 2003).

Some species, such as *H. nigricaulis*, produce specialised vegetative propagules attached to stems of mature plants (Cambridge et al. 1983; Thomson et al. 2016; Thomson et al. 2015) (Fig. 8.4c). These vegetative propagules develop from the upright stems and consist of one or more shoots attached to a horizontal ‘rhizome-like’ branch that bears roots (Cambridge et al. 1983). The vegetative propagules of *H. nigricaulis* readily detach from the parental plant and studies have shown that these can remain viable and actively grow for several months in the water column, suggesting the potential for long distance dispersal (Thomson et al. 2015).

Genetic studies on the spatial distribution of genotypes in meadows provides the means to directly identify clonal genotypes that may have dispersed and recruited through vegetative fragments. Studies in several species have shown that the same multilocus genotype can be sampled at multiple sites within a meadow and between meadows. At small spatial scales (<10 m) it is expected this results from horizontal rhizome extension, however at larger spatial scales (100s m to km) the detection of the same multilocus genotype may result from dispersal and recruitment of vegetative fragments. For example, in *Z. muelleri*, the sharing of identical multilocus genotypes has been reported between sites within meadows separated by between 20 and 50 m, however, the authors found no sharing of genotypes between meadows separated by 9–16 km (Sherman et al. 2012, 2016). In *P. australis*, the sharing of multilocus genotypes has been reported between populations on the east coast of Australia separated by 45–150 km (Evans et al. 2014), while in Western Australia populations separated by 0.4–20.6 km have been shown to share the same multilocus genotype (Sinclair et al. 2014a).

The sharing of the same multilocus genotype between populations either infers long distance dispersal and recruitment of fragments occurs in some species, or that clones vegetatively grown across large areas over centuries to milennia. However, the use of molecular methods to detect dispersal and recruitment of clonal propagules has a number of limitations. As most seagrass species also reproduce sexually, most populations consist of a large number of diverse genotypes, yet in any given study only a small fraction of them can be sampled. The probability of detecting genotypes that may have established via the dispersal of vegetative fragments is therefore vanishingly small. The ability to correctly identify clones that have dispersed between populations will also be dependent on the sensitivity of the marker system used, the diversity of the population sampled and the intensity of the sampling regime. Highly variable microsatellite markers are typically used to identify the number of unique multilocus genotypes sampled, however, genotypes consisting of common alleles may still be generated through sexual reproduction. For example, in a study by Sinclair et al. (2014b) on levels of outcrossing in *P. australis*, they found that 3–7% of embryos genotyped at seven polymorphic loci had identical multilocus genotypes. These identical genotypes most likely result from the limitation of the marker system to differentiate similar multilocus genotypes and suggests that any inferences about the recruitment from vegetative fragments in these populations needs to be treated with some caution. The probability that the same multilocus genotype has arisen independently through sexual reproduction in two or more individuals can be tested (Waits et al. 2001), allowing some confidence in whether the genotype is likely to represent the dispersal and recruitment of a vegetative fragment. The development of SNP based approaches offers potentially greater power and resolution in detecting the sharing of multilocus genotypes, although the large number of loci used by this approach may introduce additional complications due to the presence of somatic mutations at several SNP loci that can generate unique multilocus genotypes between individuals that are clonally derived. While a few studies have used SNP markers to assess population structure and adaptive divergence (Oetjen et al. 2010; Oetjen and Reusch 2007), to date studies using 100s to 1000s of SNP markers for assessing genotypic diversity in seagrasses has not been carried out but is likely to significantly increase our power in detecting dispersal of vegetative fragments (York et al. 2017).

### *8.3.3 Pseudovivipary*

Pseudovivipary in seagrass involves the formation of asexually produced plantlets growing from inflorescence peduncles and appears to involve the reversion of the floral spikelet to a vegetative propagule (Ballesteros et al. 2005; Sinclair et al. 2016b). Pseudovivipary has only been described in two seagrass species, both from the same genus *Posidonia*. The two species for which pseudovivipary has been reported are *P. oceanica* in the western Mediterranean (Ballesteros et al. 2005) and *P. australis* in Western Australia (Sinclair et al. 2016b). Pseudovivipary does not a widespread reproductive strategy across these species ranges and appears to occur in populations experiencing low levels of sexual reproduction and therefore may be an adaptation to suboptimal environments (Sinclair et al. 2016b). The presence of fruit and plantlets in the same inflorescence has been observed in both species and suggests that pseudovivipary is facultative. While the exact environmental triggers and genetic mechanisms controlling pseudovivipary are unknown, Sinclair et al. (2016b) suggested that fluctuating water temperatures might play a role by limiting flower production, and hence the amount of pollen available for outcrossed sexual reproduction.

## 8.4 Dormancy, Seed Banks, and Seed Viability

### *8.4.1 Seed Dormancy*

Seed dormancy is the inability of viable seeds to germinate under favourable conditions (Bewley 1997). The presence of seed dormancy allows species to disperse and develop seed banks that regenerate at different spatial and temporal scales. Seed dormancy and seed banks play an important role in species persistence, providing an avenue for recovery after disturbance and facilitating regeneration across generations (Fenner and Thompson 2005). In terrestrial systems, dormancy has been extensively studied and seeds can remain dormant for over 1000 years (Fenner and Thompson 2005), however dormancy in seagrass has received little attention despite the paucity of knowledge being identified over a decade ago (Orth et al. 2000) and more recently for Australian species in particular (York et al. 2017).

Seagrass seeds can be classified into three groups depending on seed anatomy and ecology (Kuo and Kirkman 1996; Orth et al. 2000, Table 8.2). The first two groups include viviparous species, such as *Amphibolis*, and those with membranous seed coats such as *Posidonia*. These species lack any dormancy period or seed bank, instead dispersing and developing directly from the adult. Species with hard seed coats make up the third group. Hard seed coats facilitate a dormancy period and include many prominent Australian genera including *Zostera*, *Halophila* and *Halodule*. Dormancy can last between a week (Phyllospadix, Reed et al. 1998) to more than 4 years (Syringodium, McMillan 1983b) depending on the species and environmental conditions. In terrestrial systems dormancy is broken by environmental, physical or physiological factors. Little research has been dedicated to seed dormancy and the mechanisms that break dormancy in seagrasses, with more research being focused on seed germination (Orth et al. 2000). There is some evidence that seagrass dormancy is initiated during seed development and therefore controlled by physiological factors, but more research is needed to quantify the onset and control of seed dormancy (Orth et al. 2000; York et al. 2017).

**Table 8.2** Comparison of seed types and seed banks characteristics from different seagrass genera

| Class | Genus | Fruit/seed covering | Dormancy | Seed bank |
|---|---|---|---|---|
| 1 | | | | |
| | *Enhalus* | Membranous | Not distinct | None |
| | *Posidonia* | Membranous | Not distinct | None |
| | *Thalassia* | Membranous | Not distinct | None |
| 2 | | | | |
| | *Amphibolis* | Viviparous | Not distinct | None |
| | *Thalassodendron* | Viviparous | Not distinct | None |
| 3 | | | | |
| | *Cymodocea* | Hard | Distinct | Transient |
| | *Halodule* | Hard | Distinct | Persistent |
| | *Halophila* | Hard | Distinct | Persistent |
| | *Phyllospadix* | Hard | Distinct | Transient |
| | *Syringodium* | Hard | Distinct | Persistent |
| | *Zostera* | Hard | Distinct | Transient |

Adapted from Kuo and Kirkman (1996) and Orth et al (2000)

### *8.4.2 Seed Banks*

Seeds that are viable but remain ungerminated in the sediment are known as the seed bank. The prevalence and persistence of seed banks allows plants to invest in future regeneration, avoid competition with adults and allow for recovery after disturbance events (Kalisz and McPeek 1992). The size and persistence of seed banks varies significantly among species, environmental conditions, flowering and germination rates, and predator abundances (Fenner and Thompson 2005). The length of time seeds are maintained in the seed bank can be critical for population persistence. Transient seed banks (those that last less than 1 year) are replenished annually via flowering, whereas persistent seed banks last for longer than 1 year allowing recovery over longer time periods (Thompson and Grime 1979). The nature of the seed bank is often reflected in reproductive strategies and environmental conditions where annual flowering creates transient seed banks but irregular flowering facilitates persistent seed banks. Seagrass seed banks show a variety of characteristics, however, there remains significant knowledge gaps many species (Orth et al. 2000; York et al. 2017).

Similar to terrestrial systems, seagrass seed banks are variable in both space and time (Fenner and Thompson 2005; Orth et al. 2000). For example *H. uninervis* seed densities ranged between 100 and 9000 seeds/m$^2$ across patches, with 87% of the variability occurring within patches (Inglis 2000a, b). In *H. nigricaulis*, seed densities in Port Phillip Bay varied between 13 and 10,000 seeds/m$^2$ (Smith et al. 2016b) but the synonymous *Heterozostera tasmanica* in Western Australia did not exhibit any seed bank over a three year period despite prolific flowering during one of those years (Campey et al. 2002). Seed banks are not necessarily related to flowering density (Campey et al. 2002) and a high proportion of seeds are lost to natural mortality with only a small proportion contributing to the overall seed bank (Harrison 1993). Micro topography of the sediment surface can cause seeds to aggregate in small depression along the surface (Inglis 2000b) but at larger scales environmental factors affecting seed production are likely to be more important in determining the accumulation of seeds in the seed bank. Across temporal scales transient seed banks from species such as *Z. marina* have greater seed abundances immediately after flowering but are exhausted as seeds germinate and are replenished during the next flowering season (Jarvis and Moore 2010; Lee et al. 2007). Similarly, *H. decipiens* produces seed banks in tropical Western Australia that allow this species to persist at depths between 8 and 15 m under extreme low light during the wet season of November to March and germinate to produce extensive and highly reproductive meadows in these environments during April to November (Hovey et al. 2015). Other species such as *H. nigricaulis* have persistent seed banks that show little variation seasonally, but can vary annually (Smith et al. 2016b). More long term monitoring is required to determine persistence of seed banks across species and time scales.

Seed banks are critical to seagrass survival, if seeds persist and remain viable until the next reproductive cycle they can act as a recovery mechanism in the event of a major disturbance (Orth et al. 2000). Seed banks have been credited with the recovery of *Zostera* habitats in the Northern Hemisphere (Becheler et al. 2010; Lee et al. 2007; Olesen et al. 2004; Zipperle et al. 2009) and are vital for deep water ephemeral and annual species such as *Halophila* to ensure regeneration (Hammerstrom et al. 2006; Hovey et al. 2015; Morita et al. 2007; Rasheed et al. 2014). However the importance of seed banks for recovery can vary across species, habitats and life history traits. For instance, seed banks in deep *Halophila* habitats provided an important source of recovery in Queensland but nearshore *H. uninervis*, *H. nigricaulis* and *Z. muelleri* showed little recovery from seeds from small disturbances in Queensland, NSW and Victoria (Macreadie et al. 2014; Rasheed 2004; Rasheed et al. 2014; Smith et al. 2016a).

Seed banks can also influence germination and seedling success. Seed density within the seed bank can play a major role in seedling emergence where emergence decreases as density increase (Grundy et al. 2003). The role of seed density on seagrass seedling success have provided contrasting results. Seedling emergence from the sediment decreased significantly as seed density increased in laboratory experiments of *Cymodocea* (Balestri et al. 2010) but densities of *Z. marina* seeds showed no effect on germination or emergence (Orth et al. 2003).

### 8.4.3 Seed Viability

Viable seeds, those capable of germination in the right conditions, are fundamental to a functioning seed bank but decrease over time as seeds germinate, are predated on or die (Bradbeer 1988). Understanding factors influencing seed viability is not only important for natural populations, but also for restoration efforts where seagrass seeds need to be stored for extended periods. Viability of *Z. marina* seeds can decrease to less than 10% in the first 6 months after seeds are set in the field (Jarvis et al. 2014) but can remain as high as 31% after 4 years in laboratory conditions (Dooley et al. 2013). Similarly, laboratory studies of *H. uninervis*, *H. wrightii* and *Syringodium filiforme* found that seeds were capable of germination after 3 years in storage, while *H. engelmannii* and *H. decipiens* continued to germinate after 18 months (McMillan 1991). In contrast, only 58% of *Z. muelleri* seeds were found to be viable after 50 days, and none were viable after 18 months reflecting the transient nature of the seed bank (Conacher et al. 1994a). In the field *Z. noltii* has been shown to germinate from seeds that have spent 3 years in the seed bank (Zipperle et al. 2009). Factors controlling viability can be both environmental, such as temperature and burial depth, and physiological, such as seed size and seed coat composition. In the few studies to investigate the role of habitat on seagrass seed viability, seeds in coarse sediment retained higher viability than those in fine sediment, which may be attributed to higher nutrient levels in finer sediments (Jarvis and Moore 2015; Stubler et al. 2017). In a landscape context, smaller patches (2.5 $m^2$) have been shown to produce more viable seeds than larger patches (Stubler et al. 2017) but further research is needed to determine what causes viability to decline in seagrass seeds and how it varies across populations.

## 8.5 Germination Patterns and Germination Stimuli

### *8.5.1 What Is Seed Germination?*

Successful seed germination results from an interaction between physiological and genetic factors (internal), and environmental factors (external), including sediment, light, salinity and temperature (Baskin and Baskin 2014). While the interaction of these internal and external factors on germination is well established for several terrestrial species (Foley 2001; Gutterman 1994; Hilhorst and Karssen 1992), little work has been done to determine the precise physiological mechanisms and external and internal factors involved in seagrass seed germination (Inglis 2000a; Orth et al. 2000, 2006). To date, the majority of seagrass germination studies have focused on processes that affect one of the final stages of the germination process, the emergence of the radicle from the endosperm (i.e. seed coat).

The broad objectives of most seagrass seed germination studies have been to relate seed germination to various abiotic and biotic stimuli and to quantify the consequences of germination timing on population dynamics and resilience (Baskin and Baskin 2014; York et al. 2017). Quantifying these relationships under natural conditions for seagrass species requires information on seed physiology, spatial and temporal variations in environmental conditions across a range of scales (both water column and sediment) and interactions between these factors from the period of seed production until germination (Baskin and Baskin 2014; Inglis 2000b; Orth et al. 2000, 2006). Additional consideration of inter and intraspecific variations in germination and viability, and links between genetics and local adaptation as drivers of these patterns are also focal points of seed germination research (Jarvis et al. 2012, 2014; van Lent and Verschuure 1994).

The following section will focus only on the process of seed germination rather than seedling growth and establishment. As such seagrasses found in the *Posidonia* and *Amphibolis* genera will be excluded, as seeds germinate immediately after fertilization while still attached to the parent plant (Kirkman 1999; Kuo and Kirkman 1990).

### *8.5.2 Environmental Cues*

Seed germination has been described as a potential limiting stage in sexual reproduction in angiosperms due to the variety of biotic and abiotic factors that affect seed survival, germination and seedling establishment (Chambers and MacMahon 1994; Harper 1977). Seed loss due to predation, disease, burial below germination depths, failed germination or export out of the system via dispersal processes, are common across many systems (Harper 1977). Seagrasses are capable of dealing with potentially high seed mortality rates through either the production of large numbers of seeds annually (Orth et al. 2006) or the development of viviparous seedlings (den Hartog 1970). However, both strategies rely on dispersal to and deposition in ‘safe sites’ (Harper 1977).

Development of ‘safe sites’ occurs when the microenvironment immediately surrounding the seeds contains the required signals to break seed dormancy and initiate germination (Baskin and Baskin 2014; Woodin et al. 1998). Environmental cues that influence germination can vary over small distances in the sediment matrix (Inglis 2000a) and with changes to and interactions between the physical and biological environments (Orth et al. 2006).

### *8.5.3 Temperature*

The timing of seagrass seed germination varies among species and ranges from specific germination seasons, where germination is restricted to a few months at a time (e.g. *Z. muelleri*, Peterken and Conacher 1997), to continuous seed production and germination throughout the year (e.g. *C. rotundata*, McMillan et al. 1982). Species-specific germination seasons can be attributed to temperature stratification requirements where seagrass seeds need to experience a prolonged period of either warm or cold temperatures to break dormancy and induce germination (Baskin and Baskin 2014). For example, *Z. muelleri* seeds germinate primarily between April and July in Moreton Bay Queensland (Peterken and Conacher 1997) and from

August and February further north in Gladstone after water temperatures have decreased seasonally (Bryant et al. 2014). Many *Halophila* species require prolonged periods of warmer temperatures ranging from 24–30 °C for 30–180 days before dormancy is broken and germination occurs (Kuo and Kirkman 1992; Kuo et al. 1993; McMillan 1988a, b; McMillan and Soong 1989).

Within seagrass populations, seeds that do not experience dormancy have a higher mean (±SE) optimum germination temperature (24.2 ± 1.6 °C) than those after dormancy is broken [18.0 ± 1.0 °C (Baskin and Baskin 2014)]. For species with no dormancy at seed maturity (e.g. *E. acoroides*) germination can occur immediately after seed production, which is early summer for the majority of Australian seagrass populations (Bonifacio and Montano 1998). Species in which seeds remain in a dormant state for a period of time may not germinate until subsequent autumn or spring seasons, and after temperatures have been reduced or increased to the extent necessary to release the seeds from dormancy [e.g. reduction from 26 to 16 °C for *Z. muelleri*, Brenchley and Probert (1998)]. For both dormant and non-dormant seeds, extreme seasonal temperatures can also restrict or delay germination (Kuo et al. 1990; McMillan 1983b).

### *8.5.4 Light/Dark Requirements*

Of the 72 described seagrass species (Short et al. 2007, 2011) the light/dark requirements for seed germination have only been explored for seven species (Baskin and Baskin 2014). Of those, only two Australian seagrass species, *H. tricostata* and *H. decipiens* have shown a light requirement for germination (Kuo et al. 1993; McMillan 1988a), however, *H. spinulosa* shows no light requirement (Birch 1981). The quality of light has also been shown to affect germination of *T. hemprichii*, *H. ovalis and Z. marina* seeds (Soong et al. 2013; Strydom et al. 2017; Wang et al. 2017). For instance, 50% of *T. hemprichii* seeds illuminated under white or blue light at 50 µmol/m$^2$ s germinated while only 21% of seeds treated under red light of the same intensity germinated (Soong et al. 2013).

The mechanism behind the light cue for, or inhibition of, seagrass seed germination is not well understood. For those species that germinate only after exposure to both light and dark conditions, the changing light environment is hypothesized to signal appropriate burial depth for germination *(e.g. Ruppia maritima*, Kahn and Durako 2005). A similar response may explain the photo-inhibition of *Halophila stipulacea* seed germination where exposure to 90% photosynthetically active radiation (PAR) resulted in significantly reduced seed germination compared to seeds exposed to 20% PAR (Malm 2006). Removal of photo-inhibition through a high concentration of suspended sediments in the water column has been hypothesized as the driving factor for the germination of *Z. muelleri* seeds following a large-scale decline in seagrass area in the Sandy Strait, Queensland (Campbell and McKenzie 2004).

### 8.5.5 Salinity

Of the environmental factors influencing seed germination determined to date, the effects of lower salinity increasing germination are the most universal (Orth et al. 2000). Lower salinity conditions can occur after extended periods of rainfall which can occur from autumn to spring in temperate regions in Australia (e.g. Goubin and Loques 1991) and during the wet season in tropical climates (e.g. Santelices et al. 2009) or as pulsed events following large scale rain or storm events (McKenna et al. 2015). Under laboratory conditions, germination of *C. rotundata* (McMillan et al. 1982), *Cymodocea nodosa* (Caye et al. 1992), *R. maritima* (Ailstock et al. 2010; Kahn and Durako 2005), *Z. noltii* (Alexandre et al. 2006), *H. nigricaulis* (Cumming et al. 2017) and *Z. muelleri* (Conacher et al. 1994a) can be stimulated using lower salinities.

Current hypotheses for the mechanism behind salinity effects on seed germination range from increased water absorption that results in tissue hydration and seed coat splitting (Loques et al. 1990), to effects on enzymatic pathways that ultimately trigger germination (Conacher et al. 1994a). It should be noted that when seeds are placed under field conditions, salinity effects observed under laboratory conditions are often not expressed (e.g. McMillan 1983a; Orth and Moore 1983). This suggests that salinity ranges typically used in laboratory studies are not often observed in situ [e.g. between 0 and 10 psu (Conacher et al. 1994a; Cumming et al. 2017; Loques et al. 1990)] and that the timing of low salinity events does not often co-occur with germination seasons. There is also evidence that high germination at low salinities may have a negative effect on seedling morphology and growth compared to higher salinities (Xu et al. 2016). Therefore, the role of salinity cues in seagrass seed germination under natural conditions should not be overstated and is still not well understood.

### 8.5.6 Dissolved Oxygen

Dissolved oxygen concentrations decrease quickly in the sediment profile with increasing burial depth (Fenchel 1969). The depth of the redox potential discontinuity, or the interface between sediments dominated by aerobic processes and sediments dominated by anaerobic processes, varies with sediment organic content, grain size, water column oxygen content, sedimentation rates and temperatures (Diaz and Rosenberg 1995; Pearson and Rosenberg 1978). Physical diffusion of oxygen from the water column into the sediment can be limited to only a few millimetres in fine sediments with high organic content (Revsbech et al. 1980) or increase to centimetres in environments with coarser sediment or areas with high amounts of bioturbation (Aller 1982).

The effect of sediment dissolved oxygen concentrations on seagrass seed germination has primarily been investigated for *Zostera* species (Moore et al. 1993;

Brenchley and Probert 1998). In *Z. muelleri* anaerobic conditions resulted in greater germination, and shorter times to germination, compared to aerobic treatments (Brenchley and Probert 1998). It is hypothesized that the surrounding oxygen environment may serve as a proxy for burial depth, with delays in germination under aerobic conditions allowing more time for bioturbation or physical processes to move the seed deeper into the substrate (Moore et al. 1993). Deeper burial depths associated with anoxic conditions may allow for greater root development prior to seedling emergence and help secure the seedling and provide immediate access to sediment nutrients. However, this hypothesis requires additional testing as a threshold may exist where seeds buried at greater depths do not have sufficient energy reserves to emerge from the sediment surface resulting in seed mortality (Granger et al. 2000; Jarvis and Moore 2015).

### *8.5.7 Sediment Conditions and Burial Depth*

The direct impact of sediment on seagrass seed germination is not well understood. Sediment characteristics including organic matter content, grain size, and pore water nutrient concentrations have been shown to significantly impact terrestrial angiosperms (Fenner and Thompson 2005). Sediments with more organic matter often contain a greater proportion of silt and clay sediments, the presence of which reduce oxygen exchange with the water column resulting in anoxic sediment conditions and greater pore water nutrient concentrations (Koch 2001; Short 1987). Both anoxic conditions and greater nutrient concentrations have been shown to increase germination in *Z. marina* (Moore et al. 1993; Probert and Brenchley 1999; Tanner and Parham 2010), although the impacts on other seagrass species are not well understood.

While few seagrass seed germination studies focus on the effects of sediment on germination, a recent study has shown that *H. nigricaulis* germination is greater in fine compared to coarse sediments, and decreases with increasing burial depth (Cumming et al. 2017). These results are similar to those of *Z. marina* which has a shorter time to germination and greater overall germination in fine compared to coarse sediments (Tanner and Parham 2010; Van Katwijk and Wijgergangs 2004) and at shallow (1–2 cm) compared to deep (5 cm) burial depths (Granger et al. 2000; Jarvis and Moore 2015; Wang et al. 2016). The lack of germination at deeper depths may be related to the absence of germination cues or physiological limitations of the seed (Nonogaki et al. 2010). Seeds buried at deeper depths require a longer hypocotyl than shallower seeds to emerge from the sediment surface. As the cotyledon provides the oxygen necessary for the survival of seedlings, any delay in the emergence of the cotyledon may result in mortality (Churchill 1983, 1992) due to the gradual reduction in energy stored in the embryo during the germination process (Kuo and den Hartog 2006; Sugiura et al. 2009).

### 8.5.8 Scarification

For germination to occur the embryo has to project enough force to rupture the seed coat (Nonogaki et al. 2010). This occurs when either the growth potential of the seed embryo increases (i.e. in response to an external cue), the mechanical resistance of the seed coat decreases or both occur simultaneously. Laboratory studies where the seed coats were either imbibed or removed completely have consistently resulted in greater germination than non-modified seed coats [*Z. muelleri*, (Conacher et al. 1994a); *Z. marina*, (Harrison 1987); *C. nodosa*, (Caye et al. 1992)]. The sculptured seed coat of *H. ovalis* with raised sections has been hypothesized to increase surface friction between the seed coat and the substrate, which may result in a reduction of the mechanical resistance of the seed coat to germination (Birch 1981; Kuo and Kirkman 1992). However, germination studies of this species have shown no significant differences in germination compared to *H. engelmanii*, *H. decipiens*, and *H. spinulosa* when seed coats were intact or removed (Birch 1981; McMillan 1976; 1988a).

### 8.5.9 Interactions

Interactions between germination stimuli can significantly affect minimum time to germination and maximum germination of seagrass seeds (Brenchley and Probert 1998; Conacher et al. 1994a; Moore et al. 1993; Ungar 1995). For example *Z. muelleri* expressed different germination responses to temperature and oxygen conditions depending upon salinity treatment (Brenchley and Probert 1998). Anaerobic conditions enhanced *Z. muelleri* germination overall; however germination did occur in aerobic conditions if seeds were exposed to low salinities (0 psu compared to 15 or 30 psu) and 16 °C water temperatures. Interactions between low salinities and low temperatures provided the necessary cue to germinate even when anaerobic germination cues were not present.

Germination of seagrass seeds under laboratory settings decreases under similar conditions when seeds are buried in a substrate treatment compared to seeds exposed to water only treatment (Jarvis and Moore 2015; Moore et al. 1993). Sediment characteristics or unknown physical processes associated with burial seem to be overriding germination cues expressed by seeds when in water only, indicating another layer of interactions which need to be quantified for a greater understanding of germination across seagrass species.

## 8.6 Dispersal and Recruitment of Sexual and Asexual Propagules

The importance of dispersal of seed and vegetative fragments is inherently difficult to measure in situ in the sea, and only a few studies have characterize the tails of dispersal curves that define long distance dispersal (LDD) events (e.g. Kendrick et al. 2012; Nathan et al. 2008). In general, LDD events are stochastic in time and space, and play a role in processes with longer evolutionary time scales, such as population genetic connectivity, responses to climate change, metapopulation dynamics, large-scale disturbance, and speciation (Cain et al. 2000; Kinlan et al. 2005). Recruitment from seeds and vegetative fragments are equally difficult to measure, largely due to the small window of recruitment, the stochastic nature of dispersal and recruitment, the heterogeneity in recruitment sites, difficulty in identifying recruits, and generally low levels of success (Kirkman 1999; Olesen et al. 2004; Rivers et al. 2011).

### *8.6.1 Physical Dispersal of Seeds*

Seagrasses invest significant amounts of energy in sexual reproduction, producing seeds and propagules that are capable of LDD (Kendrick et al. 2012). Dispersal distance estimates vary from a few meters for negatively buoyant *Z. marina* seeds (Orth et al. 1994), to tens or hundreds of kilometres for the fruit of *Enhalus*, *Thalassia* and *Posidonia* (Kendrick et al. 2012; Lacap et al. 2002) or seed bearing vegetative fragments of *Zostera* (Harwell and Orth 2002). However, we need more than these few observations and predictions of seed transport to more broadly assess connectivity, and specifically much more information on how far and how often seeds are transported from their parent plant, the survival rates of settled seeds, and the proportion that recruit not only into the adult population, but in adjacent areas.

Seagrass species that have small negatively-buoyant dormant seeds that are released on or in the sediment and form seed banks are dispersed by either transport in the bottom boundary layer of the ocean or as bed load transported by sediment itself. For example, there is evidence that annual *H. ovalis* meadows off the coast of Florida in deeper waters can move hundreds of meters between years, demonstrating the role of sediment movement and winnowing on connectivity in this species (Bell et al. 2008). However, the dispersal distances of seeds at the sediment surface are generally orders of magnitude smaller than those that float at the air-water interface (Kendrick et al. 2012), although inflorescences and seeds can be carried some distance when whole plants are uprooted and dispersed relatively long distances during storms, as suggested by Bell et al. (2008). Predictive modelling of seed dispersal of negatively-buoyant seeds still remains a major knowledge gap for seagrasses. This is, however, an emerging area of research in terrestrial systems, one that also needs investigation within aquatic systems (estuarine and coastal). A recent publication on secondary seed movement describes and models a similar process in terrestrial vegetation in deserts as a result of vegetation tumbling in the wind or seeds being moved with sediments during floods (Thompson et al. 2014).

Fruit dispersal on the air-water interface by floating fruit has the potential to produce dispersal in the order of hundreds of km (Kendrick et al. 2012). Some examples are those of Källström et al. (2008), who applied a model to predict transport distances up to 150 km for *Z. marina* floating ripidia along the Swedish coast. Erftemeijer et al. (2008) inferred similar dispersal distances when simulating the dispersal of floating *Z. marina* reproductive shoots in the Wadden Sea, Netherlands, using a much more sophisticated three-dimensional hydrodynamic model, driven by a combination of surface currents from the model plus an additional assumed windage contribution of 3% of the wind speed. Recent advances in understanding the physical mechanisms of dispersal of Australian *P. australis* fruits at the water surface included the role of windage through direct field observations (Ruiz-Montoya et al. 2012). This windage, coupled to a hydrodynamic and particle transport models (Ruiz-Montoya et al. 2015) demonstrate the potential for high levels of contemporary connectivity through multiple dispersal events of *P. australis* fruit (20–40% of floating fruit) between locations 10 km apart, including rare LDD events (>90 km for <5% of fruit). Clearly, the capacity for connectivity through seed dispersal among populations hundreds of kilometres apart exists for those species that have floating fruit, ripidia, or vegetative fragments containing seeds. How this relates to successful recruitment can be addressed to a degree by population genetic studies that assess connectivity and genetic diversity (Evans et al. 2014; Sherman et al. 2016; Sinclair et al. 2014a, 2016a; Smith et al. 2013).

### 8.6.2 Biotic Vectors of Seed Dispersal

Biotic dispersal has the potential to be an important vector for long distance dispersal in seagrasses (McMahon et al. 2014). Seagrass beds support a rich diversity of vertebrate and invertebrate fauna (Larkum et al. 2006), many of which are capable of ingesting and excreting whole seeds (Table 8.3 in Orth et al. 2006). Seeds in stomach samples are greatest when seeds are most abundant in the field (Adams 1976; O'Brien 1994; Wassenberg and Hill 1987; Wassenberg 1990). Sumoski and Orth (2012) showed that several species of fish, a turtle and waterfowl all could consume and excrete whole viable seagrass seeds suggesting that biotic dispersal could occur, and that depending on gut passage time and movement within or between beds, dispersal distances could be large (McMahon et al. 2014). Tropical marine mega-herbivores (dugong and green turtles) are also capable of ingesting and excreting viable seeds of several seagrass genera (*Zostera*, *Halodule* and *Halophila*) and based on digesta period and movement patterns, have the potential to disperse seeds among meadows locally when foraging and over

**Table 8.3** Published seagrass recruitment and germination rates (# $m^{-2}$ $year^{-1}$) for non-dormant and dormant seeds, respectively

| Species | Location | Germination or recruitment rate (# $m^{-2}$ $year^{-1}$) | Reference |
|---|---|---|---|
| **Buoyant fruit (non-dormant, dispersal at water surface)** | | | |
| *Enhalus acoroides* | Bolinao, Philippines | 0.043–0.081 $m^{-2}$ $year^{-1}$ | Olesen et al. (2004) |
| *Enhalus acoroides* | Bolinao, Philippines | 27 seedlings $m^{-2}$ $year^{-1}$ | Rollon et al. (2003) |
| *Posidonia oceanica* | Ligurian Sea, Italy | 3.2 ± 0.4 seedlings $m^{-2}$ | Balestri et al. (1998) |
| *Posidonia oceanica* | Tuscan Coast, Italy | 2.6–3 seedlings $m^{-2}$ | Piazzi (1999) |
| *Posidonia oceanica* | Corsica, Western Mediterranean | 80 ± 15 one year old seedlings $m^{-2}$ | Balestri and Lardicci (2008) |
| *Posidonia oceanica* | Sicily, Italy | 0.13 ± 0.08 to 16 ± 1.73 seedlings $m^{-2}$ | Alagna et al. (2013) |
| *Thalassia hemprichii* | Kalayaan Island Group, Phillipines | 22–23 seedlings $m^{-2}$ | Rollon et al. (2001) |
| *Thalassia testudinum* | Florida Keys, USA | 1 year old seedling $m^{-2}$ | Whitfield et al. (2004) |
| **Seedbank forming (dormancy, dispersal within the sediment)** | | | |
| *Halophila decipiens* | Florida, USA | 7.89 $m^{-2}$ ± 3.97 $m^{-2}$ $year^{-1}$ | Hammerstrom et al. (2006) |
| *Halophila beccarii* | Kemaman, Peninsular Malaysia | 8 ± 4.8 to 160 ± 36.3 $m^{-2}$ | Zakaria et al. (1999) |
| **Seedbank forming (dormancy, dispersal from the water column)** | | | |
| *Phyllospadix torreyi* | California, USA | 15.2 seedlings $m^{-2}$ | Buckel et al. (2012) |
| *Zostera marina* | Willapa Bay, USA | 0.1–7 seedlings $m^{-2}$ | Wisehart et al. (2007) |
| *Zostera marina* | Yaquina River Estuary, USA | 0 | Boese et al. (2009) |
| *Zostera marina* | Chesapeake Bay, USA | 1–40% of seedling establishment | Marion and Orth (2012) |
| *Zostera marina* and *Z. noltii* | Oosterschelde Estuary, Netherlands | 12% of the seedlings successfully established | Harrison (1993) |
| *Zostera noltii* | Wadden Sea, Germany | Frequent recruitment (12% of seedbank) | Zipperle et al. (2009) |
| *Zostera capricorni* | South-East Queensland | 87 ± 30 to 951 ± 553 seeds $m^{-2}$ | Peterken and Conacher (1997) |

hundreds of kilometres when migrating (Tol et al. 2017). Manatees and waterfowl may also be likely candidates to disperse seagrass seeds, yet we know little of their potential to disperse seeds even if they are ingested (Tulipani and Lipcius 2014). Seeds and plant fragments have also been found in waterfowl guts or attached to external body parts suggesting they may be an important long distant dispersal agent (Baldwin and Lovvorn 1994; Figuerola and Green 2002; Figuerola et al. 2002).

### 8.6.3 *Physical Dispersal and Recruitment from Vegetative Fragments*

A major area in seagrass recruitment dynamics that is still poorly understood is whether detached vegetative fragments can contribute to connectivity among populations. Detached fragments can be generated by a variety of biotic (e.g. ray, dugong, manatee, turtle or waterfowl feeding) or abiotic (e.g. storms, boating, dredging) disturbances and can be transported either at the air-water (Hall et al. 2006) or sediment-water interface (Campbell 2003). These fragments vary in buoyancy and consequently in their dispersal distance potential (Weatherall et al. 2015). Nevertheless, they can remain viable for a period of time as noted in the fact they are successfully used in numerous restoration projects (Fonseca and Bell 1998). However, in these projects, fragments are inserted manually into the sediment and whether these fragments can be buried naturally generally remains to be conclusively shown and an area of future research. The few field studies conducted to date suggest that the probability of successful establishment of detached fragments is extremely low (Campbell 2003; Ewanchuk and Williams 1996). However without further detailed studies on the recruitment of detached fragments, it is hard to assess their role in population connectivity although similar to seeds, rare recruitment events from dispersed vegetative fragments have the capacity to maintain and potentially increase genetic connectivity among seagrass meadows.

### 8.6.4 *Recruitment from Seeds*

Information on seed germinating and recruit density has been widely reported across many species (Table 8.3), yet the contribution of these germinating seeds and recruits to meadow development and maintenance remains poorly understood (Kendrick et al. 2012, 2017). Similarly, recent work from the USA has shown that greatest expansion of *Z. marina* beds that had been monitored for over two decades occurred within 90 m of the bed edges, which could only have been accomplished by seed dispersal from the parent bed (Wilcox, unpublished).

The effect of recruitment on the population dynamics of clonal plants has been largely acknowledged as very important, but difficult to study. Different strategies have been suggested to classify recruitment in seagrass according to the frequency of seed production, dispersal range and overall contribution to existing populations. Eriksson (1989) used two contrasting categories; the first one, Initial seedling recruitment (ISR), relates to when recruitment occurs after long distance dispersal events, away from parent populations. The second strategy is referred to as repeated seedling recruitment (RSR) and relates to when seeds continuously recruit among existing adult populations. A third category was suggested called recruitment windows of opportunity, where recruitment is repeated, but infrequent and in response to environmental stimuli (Eriksson and Fröborg 1996). The first of these categories rely heavily on seed export and establishment outside the meadow, and recruitment success is dependent on the genet growing clonally. On the other hand the RSR strategy is characteristic of species that lack long distance dispersal mechanisms and where seeds recruit into the meadow and are better adapted to compete among adults. The recruitment window of opportunity strategy is an extension of these where environmental conditions, such as nutrient pulses, cause germination, growth and recruitment.

Recruitment is heavily influenced by the local biological, physical and environmental conditions. Manley et al. (2015) showed that after reproduction the majority of seeds and recruits of *Z. marina* remained either within the parent meadow or close to the edge, and the density of recruits decreased as distance from the meadow increased. Alagna et al. (2013) monitored *P. oceanica* recruits and found a survival up to 80% after two years on rocky substrates, and complete mortality over sandy substrates. Contrastingly, Balestri and Lardicci (2008) surveyed one year old recruit densities of *P. oceanica* in a sheltered area and found no differences between substrate, but found clumps with high recruit densities that demonstrate the importance of microhabitats on successful recruitment (Rivers et al. 2011).

## 8.7 Management and Conservation of Seagrass Populations

Seagrasses are important components of coastal ecosystems that act as a refuge to numerous organisms and provide multiple key environmental services. Anthropogenic related activities such as pollution, eutrophication, coastal development and dredging among other activities have led to substantial declines in these ecosystems worldwide (Waycott et al. 2009). Management and protection of seagrass habitat has taken place in order to protect existing species or ecosystems and inherently conserve the services provided by them, which have been valued at ~1.9 US trillion for nutrient recycling alone (Costanza et al. 1997). In order to successfully manage and mitigate losses on these ecosystems we first need to know the state and extent of existing populations, gain a good understanding of natural population dynamics, and most importantly the processes that affect them. We also need to develop cost-efficient restoration techniques that maximise recovery over large areas and result in long-term viable populations.

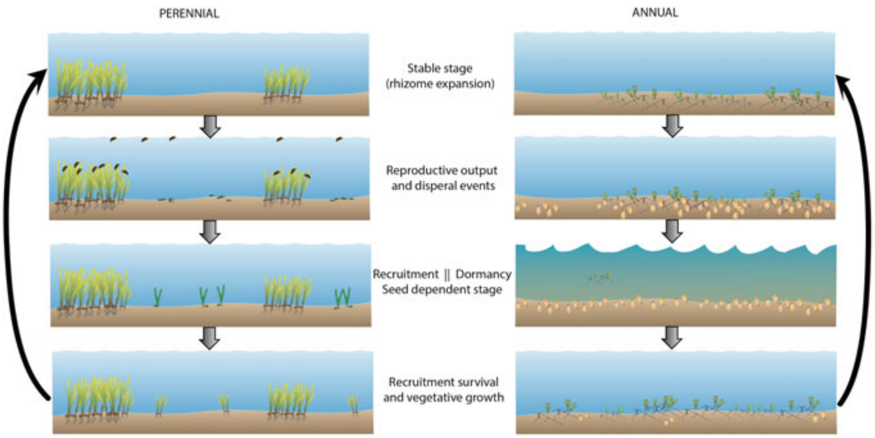

**Fig. 8.5** Comparison of different seed reliance on the population dynamics for and perennial and annual species

Long term monitoring and mapping of seagrass populations have identified changes in the abundance and distributions of seagrasses among years and decades (e.g. Kendall et al. 2004; Kendrick et al. 2000, 2002). In a review of European monitoring projects, Marbà et al. (2013) found that as of 2000 onwards, most European countries have adopted monitoring programs and the majority of these programs focussed on biomass, % cover or shoot density as indicators of stress and few addressed recruitment from seeds and vegetative fragments. These methods do not accurately reflect the changes in abundance and distribution for fast growing annual populations, such as *Halophila* species, a common genus in the tropics that can spread over large areas of the deep subtidal (Fonseca et al. 2008; Long et al. 1993; York et al. 2015). To address this discrepancy between life-history characteristics and monitoring methodologies, Hovey et al. (2015) proposed the incorporation of seed bank monitoring and species specific seasonal growth cycles in designing monitoring programs for fast growing and ephemeral species (see Fig. 8.5).

Seagrass ecosystems are continuously changing; Bell et al. (1999) illustrated the dynamics of seagrass meadows by monitoring almost 5 ha of monospecific meadows of *H. wrightii* in Florida. This study monitored seagrass gaps over a two year period and found that gaps represented 2.4–5.7% of the seagrass landscape with gaps ranging in size from 10 to 305 m$^2$. Many of these gaps were colonized within a 6–18 month period, however, gap area and persistence were related to the number of extreme sedimentation events. Similarly, Almela et al. (2008) studied the patch dynamics of the much slower growing species *P. oceanica* in the Mediterranean, and showed that despite the slow growth of patches over small areas, there was still some colonization or development of new patches in the area through both rooting vegetative fragments and seedling recruitment. This highlights the importance of the consideration of both reproductive strategies on the population dynamics and also the need for methodologies to take into account the natural net gain/loss of existing meadows and not only the monitoring of fixed quadrats which do not capture the dynamics of the landscape.

Knowing that sexual reproduction makes an important contribution to seagrass population dynamics does not in itself allow us create general guidelines for conservation. This is because there is large temporal variability in reproductive output and recruitment dynamics, however, the drivers for good/bad years remain poorly studied in most seagrass species (Kendrick et al. 2017). Disturbance events are known to be important in stimulating high reproductive events in some species. For example, Balestri and Lardicci (2008) reported massive recruitment success of *P. oceanica* and hypothesised that the high flowering production followed from an abnormally hot year. Extreme events can thus impact population dynamics in different ways, but the thresholds for successful recovery are complex and also dependent on the magnitude and frequency of the disturbance events. Of particular concern for seagrass dynamics is the impact of consecutive multiple stressors that can interact to limit the ability of seagrass populations to recover. Fraser et al. (2014) documented a large loss of the seagrass *Amphibolis antarctica* in Shark Bay, Australia, after an extreme heatwave accompanied with increased frequency of floods. Similarly, Jarvis and Moore (2010) assessed the state of *Z. marina* on the Cheasapeake Bay, USA after a seagrass loss from a single event, and found a greater number of seedlings recolonizing the area. However, this caused a depletion of the seed bank with a subsequent decline in the viability of the remaining seeds (Jarvis et al. 2014).

Extreme events are not always catastrophic and are known to assist dispersal and stimulate germination of seed banks. Bell (2008) documented the movement of a seed bank over hundreds of metres after a hurricane hit the Florida region, resulting in the establishment and growth of *H. decipiens* over a previously bare area. Kendall et al. (2004) monitored deep water (10–20 m) meadows of *S. filiforme* in the US Virgin Islands, and found expansion of the beds following years of high hurricane activity. This suggests that life history strategies of some seagrass species may have adapted and benefit from extreme events (see Fig. 8.5). Overall, seed recruitment is not only species specific but is thought to be heavily influenced by the occurrence and magnitude of physical disturbances, such as the seasonal occurrence of tropical storms (Olesen et al. 2004), sediment burial events (Blackburn and Orth 2013; Valdemarsen et al. 2011), and habitat fragmentation (Salita et al. 2003; Vermaat et al. 2004). Similarly, biological factors, can operate as an environmental 'sieve' to seedling recruitment (Eriksson and Ehrlén 1992; Orth et al. 2002, 2006) through intra- and inter-specific competition among seagrass species (Duarte 2000), and predation (Fishman and Orth 1996; Holbrook and Smith 2000; Orth et al. 2007; Wassenberg 1990).

Restoration of seagrass meadows represents the last step in management. Restoration efforts have already been carried out for a number of species, primarily in relation to coastal development and other human related pressures. However, despite these efforts restoration has proven to be challenging and success has been low (van Katwijk et al. 2015). One of the best examples of successful seagrass restoration involves the restoration of *Z. marina* in South Bay (Chesapeake Bay) by adding approximately 37.8 million viable seeds to 369 individual plots ranging in size from 0.01 to 2 ha over an eleven year period (1999–2010). A survey in 2010 found that seagrass covered approximately 1700 ha and was attributed to seed exported from the original plots with subsequent germination and establishment of seedlings (Orth et al. 2012).

It is clear that seagrasses have the capacity to overcome pressures and recover from losses through clonal expansion, seed and vegetative fragment recruitment. It is thus necessary to maintain appropriate conditions locally in order to accomplish stability of the existing populations. It is also imperative to account for the spatial variability of aerial cover of seagrass meadows and the life cycle strategies of the species in question. Aerial photography and satellite images allow us to quantify meadow dynamics on a large scale (e.g. Kendall et al. 2004; Kendrick et al. 2002) but at the same time there is the need to apply the right monitoring techniques depending on the life cycle of the species in question. Perennial slow growing species are likely to find it harder to recover from large losses and thus special attention is required when disturbing these species. In contrast, ephemeral faster growing species such as *Halophila* species from tropical Australia may be capable of renewing their populations rapidly from existing seed banks (Hovey et al. 2015; York et al. 2015). Despite the significant ongoing loss of seagrass ecosystems globally, it is clear that there is an urgent need to gain a better understanding of the reproductive biology, dispersal and recruitment processes of individual seagrass species in order to provide the knowledge and tools necessary to protect and restore these ecosystems.

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# Chapter 9
# Australian Seagrass Seascapes: Present Understanding and Future Research Directions

**Gary A. Kendrick, Renae K. Hovey, Mitchell Lyons, Chris Roelfsema, Leonardo Ruiz Montoya and Stuart Phinn**

**Abstract** Seagrass seascapes are 100s $m^2$ to 1000s of $km^2$ coastal regions in nearshore, sandy to muddy benthic environments that are characterized by the presence of seagrasses. Here we explore the development of seagrass seascape research in Australia. Determining the distribution of seagrasses started with mapping their extent, but improvements in remote sensing and statistical modelling has allowed us assess the large scale spatial distribution and temporal dynamics of seagrass seascapes. We use a case study from Moreton Bay, near Brisbane, Queensland to demonstrate changes in seagrass meadows over time. Terrestrial landscape indices and their use in seagrass studies is reviewed. Some indices perform better to summarize patch to meadow scale changes in the distribution and structure of seagrasses. A case-study is then presented, comparing landscape indices calculated from observed changes in seagrass patches and meadows to a spatially-explicit model simulation, to explore the drivers for changes in the seagrass seascape's demographic processes, clonal growth and recruitment from seeds. The role of landscape structure in the movement and abundance of associated fauna in seagrass seascapes using landscape approaches is then reviewed. This is followed by a summary outlining directions for future research that combine landscape ecology and remote sensing techniques with population and community biology.

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## 9.1 Introduction

Seascape ecology is the application of landscape ecology to the marine environment, and is based on concepts and techniques developed for terrestrial systems (Robbins and Bell 1994). It is an area of study that broadly looks at spatial variation in landscapes across a range of habitat elements and space and time scales. A landscape is larger than an individual's immediately observable area and landscape studies typically address heterogeneity across landscape elements at very large spatial scales relative to the organism or process of interest (Bell et al. 2006). Landscape ecology includes understanding patterns and interactions among ecosystems within a defined area, and the way these patterns and interactions affect ecological processes. Of particular interest is the unique effects of spatial heterogeneity on biotic interactions. Spatial dynamics, or patch dynamics in marine systems has been extensively studied for many decades (e.g. Hutchinson 1953; Steele 1978; Pickett and White 1985; Levin and Paine 1974) and these studies have been a major influence in the theoretical development of terrestrial landscape ecology. More recently since the seminal paper of Robbins and Bell (1994) the explicit examination of spatial arrangement, patchiness, edge effects, movement and connectivity across landscape elements, been applied to the study of seagrasses in the marine environment, where it is now commonly referred to as ***seascape ecology***. Our intentions for this chapter are to summarize seagrass seascape studies in Australia by describing pattern through mapping, characterizing the landscape features through indices, modelling seagrass growth across landscapes and by summarizing the association and movement of mobile fauna in seagrass seascapes (Fig. 9.1).

Understanding the spatial relationships between seagrass species and their environment at a seascape scale is required to effectively manage seagrass ecosystems under increased anthropogenic pressures (Orth et al. 2006a; Kilminster et al. 2015). The issues of scaling processes that determine the survival and growth of seagrasses and associated biota to the dynamics of seagrasses in shallow near-shore coastal and estuarine environments are only just being treated systematically by marine researchers (e.g. Kendrick et al. 2008), yet large gaps remain in our knowledge of seagrass seascapes, limiting our ability to predict trends for sustainable management and conservation. This Chapter will address our present knowledge of seagrass seascapes, focusing on scales of influence both in time and space, describing seascape dynamics, determining scaling of physical and biological drivers of seascape pattern, and drivers of the movement and abundance of seagrass associated biota through seagrass seascapes.

Most studies on seagrass spatial dynamics have been conducted on relatively small scales, many focus on describing the growth rates of seagrass rhizomes measured exclusively at the scale of shoots (e.g. Brouns 1987; Williams 1990; Olesen and Sand-Jensen 1994). These results have been scaled upwards directly to the functioning of the patch and meadow (Kendrick et al. 1999, 2005a; Sintes et al. 2005; Renton et al. 2011), but there is growing evidence that seagrass seascapes are not solely driven by shoot scale interactions and scaling shoot dynamics to the

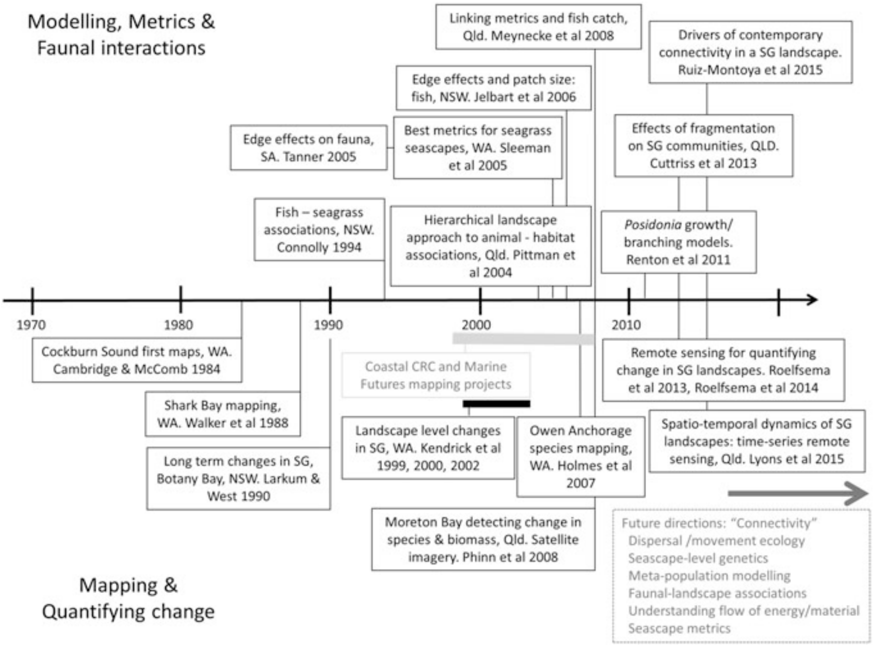

**Fig. 9.1** Major steps in the study of Australian seagrass seascapes from 1980s to present day. SG = seagrass

seascape only accounts for a small proportion of the broad scale dynamics in seagrass meadows (e.g. Kendrick et al. 2008).

Seagrass mapping of historical changes in seagrass distributions (Kendrick et al. 1999, 2000, 2002; Roelfsema et al. 2014) have demonstrated that the rate of colonization exhibited by some seagrasses is too fast for vegetative spread from the edge of existing meadows and is more likely a multi-stage process of short distance dispersal, patch establishment, patch expansion and coalescence, all working below the grain or resolution of imagery used in mapping. The relationship between broad-scale decadal changes in seagrass distributions and plant-related processes proposed as the drivers (colonization, growth, and competition between seagrass species at the shoot and meadow scale) has yet to be satisfactorily resolved (Kendrick et al. 2005a, 2008), since only a few of these mapping exercises attempted to correlate the spatial changes in seagrass landscapes to underlying processes generating that change (Fonseca and Bell 1998; Robbins and Bell 2000; Fredericksen et al. 2004a).

It is difficult to infer process from pattern (Wagner and Fortin 2005; van Teeffelen and Ovaskainen 2007) and, unlike most terrestrial systems, the missing link between pattern and process is pattern at broader scales (Kendrick et al. 2008; Ooi et al. 2014). Seagrass landscapes, even when composed of large and slow-growing seagrasses, can be highly dynamic over time scales of decades (e.g. Larkum and West 1990; Quammen and Onuf 1993; Short and Burdick 1996;

Kendrick et al. 2000, 2002; Seddon et al. 2000; Fredericksen et al. 2004b), contrary to the general statement for most of the temperate Australian seagrasses, thought to be unable to colonize at measurable rates and once disturbed rarely recover (Clarke and Kirkman 1989; Kirkman 1985).

Habitat fragmentation is increasingly common in both terrestrial landscapes and marine seascapes. The subtidal temperate regions of southern Australia support extensive seagrass seascapes that are characterized by mosaics of multi-species seagrass patches and meadows that are interspersed in sand (Walker et al. 2001; Carruthers et al. 2007). Long-term mapping studies have indicated that these seagrass seascapes exhibit spatial changes in seagrass cover and distribution (Kendrick et al. 2000, 2002) that can be defined along a continuum from many small seagrass patches interspersed in sand, to a single continuous seagrass meadow. The process of fragmentation has been described by a range of ecological, physical and anthropogenic processes, including the influence of different species of seagrass an their specific life history traits, growth and recruitment rates (Carruthers et al. 2007; Hastings et al. 2007; Kendrick et al. 2008).

Different seagrass assemblages possess unique sets of physiological and morphological characteristics, that provide them with the mechanisms necessary for persistence in particular environments and may also influence differences in the spatial organization of seagrass assemblages. As clonal organisms, seagrasses are capable of reproducing without sexual interactions. Lateral expansion and architecture of seagrass relies heavily on elongation of rhizomes (i.e. the rate of addition and size of rhizome internodes), branching pattern (i.e. the branching frequency and branching angle), and length of the rhizomes between consecutive shoots (Marba and Duarte 1998; Kendrick et al. 2005b; Sintes et al. 2005; Renton et al. 2011). Seagrass are also capable of reproducing through sexual means but, as with other clonal plant populations, seedling establishment appears to be infrequent (Inglis 2000a; Kirkman 1998 but also see Kendrick et al. 2012, 2017). The reproductive characteristics (i.e. the number of seeds released per year), dispersal and recruitment of reproductive and vegetative propagules can influence the spatial pattern of seagrass assemblages (Inglis 2000b; Hovey et al. 2015; Kendrick et al. 2012, 2017; McMahon et al. 2014), yet it is uncertain about the magnitude of the role seagrass recruitment plays in the spatial structuring of seagrass seascapes.

Mapping of seagrasses in Australia started in the 1970s but improvements in remote sensing and statistical modelling of species distributions has led to great advances in our detection of seagrasses and our understanding of the large scale spatial distribution and spatial dynamics of seagrass seascapes. We demonstrate the capacity of modern remote sensing to assess change in seagrass seascapes over time through a case study from Moreton Bay, near Brisbane, Queensland (also see the remote sensing chapter). In the 1990s and through the 2000s landscape indices were increasingly used to describe the structure and fragmentation of seagrass meadows (Fig. 9.1). Landscape indices are introduced with specific focus on their use in seagrass studies. They are also utilized in the landscape modelling case study that follows the indices section. Modelling was first used in seagrass research in the 1990s and early 2000s to assess the contributions of demographic processes (clonal growth and recruitment from seed) on emergence of pattern across seagrass seascapes. A case study is presented as a demonstration of the use of landscape modelling to demonstrate potential contributions of clonal growth and seed recruitment to observed changes to seagrass seascapes on Success and Parmelia Banks, near Perth Western Australia. Finally, we summarize a large body of Australian and international literature on the role of landscape structure in the movement and abundance of associated fauna in seagrass seascapes using landscape approaches. This is followed by a summary outlining directions for future research.

## 9.2 Mapping Change in Seagrass Seascapes

The development of seabed-mapping technologies in the last two decades (Kenny et al. 2003) has enabled the generation of accurate maps of landscape classes within coastal seascapes, like seagrass meadows, reefs and un-vegetated sand. These seabed mapping methods are useful for assessing the state of living resources, similar to that which occurs for terrestrial resources, and are increasingly in demand for a variety of applications, including: marine park placement and zoning (Friedlander et al. 2003); marine resource management (Bax et al. 1999); environmental monitoring (Kendrick et al. 2000, 2002); holistic catchment management; and integrative ecological research (Durako et al. 2002; Fonseca et al. 2002). Mapping the extent of seagrass seascapes has traditionally served as a general indicator of coastal ecosystem health (Kilminster et al. 2015) and more recently has served the analysis of spatial patterns using landscape metrics. However, an understanding of the spatial heterogeneity within meadow dynamics such as composition, density and productivity (biomass) is also important.

In the last two decades, effort has focused on developing efficient marine survey equipment and data acquisition systems to map a wide range of abiotic and biotic features on the seafloor (Kenny et al. 2003; McRea Jr. et al. 1999; Solan et al. 2003; Chap. 15). This has been augmented by the application of sophisticated statistical modeling methods to benthic datasets (e.g. multivariate analysis: Freitas et al. 2003; CARTS: Holmes et al. 2008; Hovey et al. 2012; generalized additive models: Garza-Perez et al. 2004; geostatistics: Kendrick et al. 2008; Ooi et al. 2014). However, as seagrasses are commonly found in shallow clear water, an appropriate approach to mapping seagrass extent involves using remotely sensed image data such as airborne or satellite multispectral or hyperspectral imagery.

More recently, composition and structure of seagrass meadows have been mapped as a direct function of remotely sensed image data. Historical maps of seagrass seascapes that provide composition and structure information were typically visually estimated (Young and Kirkman 1975; Hyland et al. 1989). Time series of seagrass structure may be derived from some historical aerial image data, but it was not until the 1980s that moderate spatial resolution (5–30 m pixel size) satellite image data (e.g. Landsat satellites) were available to create true time series of seagrass structure using directly comparable images which allows quantitative

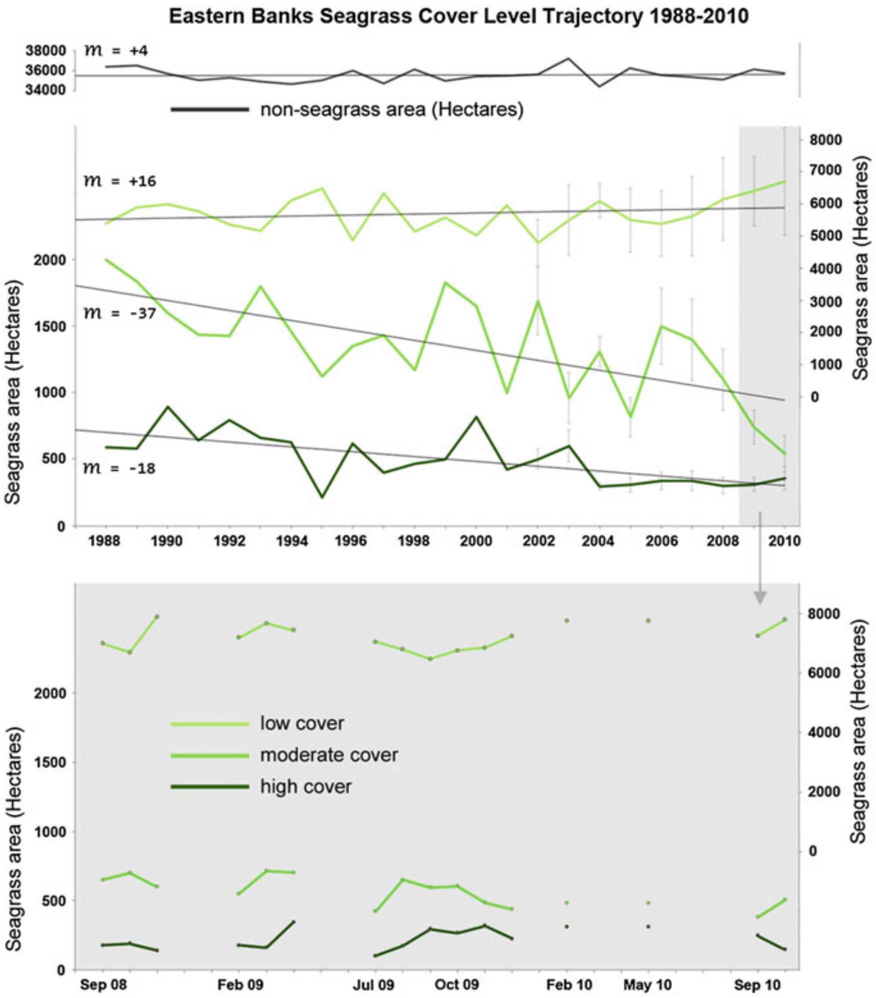

**Fig. 9.2** Annual (lower panel) versus monthly (upper panel) monitoring of the area covered by three classes of seagrass percentage cover, high (100–60%), moderate (60–40%) and low (40–0%) for Moreton Bay, Queensland, Australia (Lyons et al. 2013)

assessment over time (e.g. Lyons et al. 2013) (Fig. 9.2). In the 2000s, high spatial resolution (1–5 m pixel size) satellite image data (e.g. IKONOS, Quickbird, Worldview) became available to create time series that allows quantitative assessment of seagrass composition (e.g. Fig. 9.3, Roelfsema et al. 2014), although some rare exceptions exist for moderate resolution data (Dekker et al. 2005).

Examples of seagrass biomass mapping for one or two image dates have been common since the 1990s (Phinn et al. 2008), but time series that allow quantitative assessment of the spatial distribution and absolute weights of above ground biomass (Fig. 9.4) have only recently been demonstrated (Roelfsema et al. 2014;

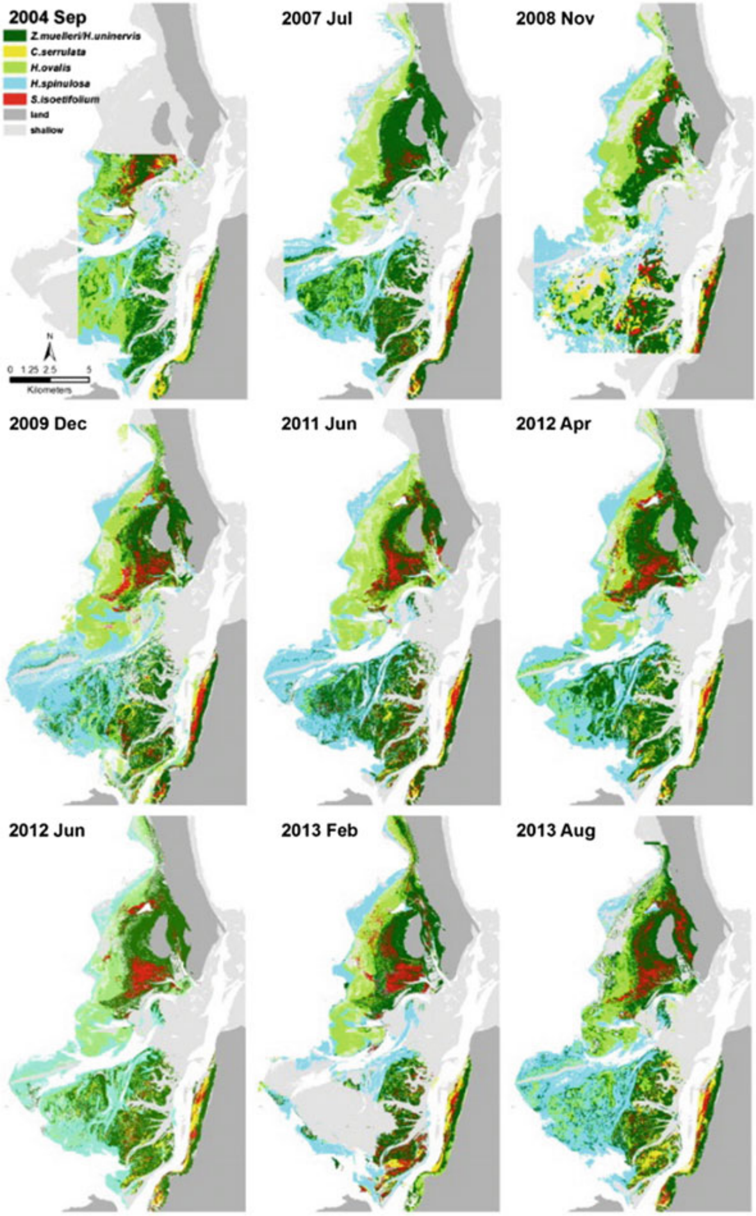

**Fig. 9.3** Annual mapping of seagrass species (composition) for Moreton Bay, Queensland, Australia (Roelfsema et al. 2014)

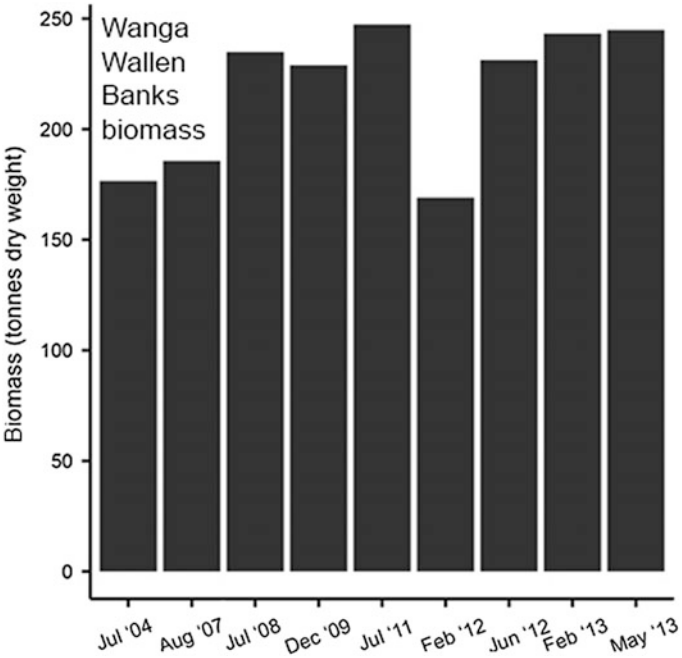

**Fig. 9.4** Annual time-series of above ground biomass for Moreton Bay, Queensland, Australia (Lyons et al. 2015)

Lyons et al. 2015). These methods have been driven by the increased interest in inventory and dynamics of coastal Blue Carbon (the carbon sequestered by seagrass, mangrove and saltmarsh ecosystems), and globally and publicly available satellite image data archives.

## 9.3 Seagrass Landscape Indices

Metrics and indices that quantify ecologically important spatial patterns are necessary for linking spatial patterns to ecological processes (Turner 1989). Real landscapes contain complex spatial patterns in the distribution of resources that vary over time; so the ability to quantifying these patterns and their dynamics is the core of landscape pattern analysis. Once an area of interest has been mapped, the seascapes are often represented visually using several different conceptual models with varying cartographic properties (i.e. spatial and thematic resolution; Wedding et al. 2011). A common representation of seascape structure is the ‘patch-matrix’ model, where the map classification is binary with focal ‘high quality’ patches embedded in a matrix of ‘lower quality’ habitat and is based conceptually upon island biogeography theory (Wedding et al. 2011). The focus of this patch-matrix model has been on patch attributes such as area (i.e. species–area relationships), biotic response to patch edges, perimeter: area ratios, patch shape, and inter-patch distances and/or isolation. From these attributes the quantifiable metric or indices used to characterize the spatial structure of seascapes were developed, stemming from the original need to quantify the complex spatial heterogeneity represented in remotely sensed images (both aerial photography and satellite imagery).

No individual index can capture the full complexity of spatial patterns, and in most cases multiple indices are required for analysing landscape configuration (Saura 2002). A set of metrics are often considered useful when they are selected for a particular objective, measured values are well-distributed over a range of scales and metrics are relatively independent. These concepts and analytical techniques in landscape ecology are well developed in terrestrial systems and provide a framework that can be readily applied to assess broad-scale seagrass patterns and disturbances (Wedding et al. 2011).

Landscape indices have been shown to be a useful tool for characterizing marine benthic communities (Garrabou et al. 1998). In most seagrass seascape studies, spatial properties relating to fragmentation or animal-habitat associations have been described with simple measures like average patch size and the numbers of seagrass patches per unit of area (Bell and Hicks 1991; Irlandi 1994; Irlandi et al. 1995; Pittman et al. 2004). More complex indices have occasionally been used such as Connectivity, Patch Dispersion (cumulative variation of Nearest Neighbour Distance), Patch Adjacency (Interspersion and Juxtaposition) and Contagion to measure various spatial attributes of seagrass seascapes (Robbins and Bell 2000; Hovel and Lipcius 2001; Santos et al 2015).

The requirements of choosing indices in fragmented landscapes were explicitly stated by Jaeger (2000). He suggested that the selection of indices should be based on: (i) the extent to which they measure fragmentation; (ii) mathematical homogeneity with increasing extent; (iii) intuitive interpretation; (iv) detection of important structural features of fragmentation; (v) comparison of regions of different grain and extent; (vi) mathematical simplicity; (vii) modest data requirements; (viii) low sensitivity to small patches; and (ix) monotonous reaction to different fragmentation phases. In 2005 Sleeman et al. reviewed the literature relating to the implementation and testing of indices specifically for the analysis of fragmented seagrass landscapes, identifying a total of 24 indices (Gustafson and Parker 1992; Riiters et al. 1995; Haines-Young and Chopping 1996; Reed et al. 1996; Schumaker 1996; Jorge and Garcia 1997; Li and Archer 1997; Gustafson 1998; Hargis et al. 1998; Kendrick et al. 1999; O'Neill et al. 1999; D'Eon and Glen 2000; Jaeger 2000; Robbins and Bell 2000; Hovel and Lipcius 2001). These 24 indices were reduced to 11; grouped according to the principle aspects of spatial pattern they measure as defined by McGarigal (2002): Area/density/edge, Shape, Dispersion, Subdivision and Connectivity.

Within these groups, individual indices were examined against the following eight criteria:

(1) Can be defined at a class-level (e.g. seagrass or sand in a shallow subtidal landscape);

(2) Specifically relate to fragmentation;
(3) Are relatively insensitive to scaling issues such as grain and extent;
(4) Have low correlation with other indices;
(5) Relate to ecological processes;
(6) Are sensitive to important structural properties;
(7) Are applicable for comparing landscapes of different areas; and
(8) Can be calculated in a raster data format.

Sleeman et al.'s (2005) analysis concluded that no single index can be used to comprehensively quantifying the complex spatial aspects of fragmentation and that multiple indices should be used which are not strongly correlated and are easily interpretable. Based on the overall performance of indices and index compatibility, Area Weighted Mean Perimeter to Area Ratio, and Landscape Division, were found to be preferred indices for providing a comprehensive assessment of spatial structure while avoiding strong correlation among indices.

Area Weighted Mean Perimeter to Area Ratio generally measures the complexity of patch shapes in terms of whether they are simple and compact or irregular and convoluted, with a perfect square patch having a value of 0.01, and specifically looks at the overall perimeter and area of a class rather than individual patches (McGarigal and Marks 1995). Landscape Division is the area weighted mean of area and is given as a probability that two randomly chosen pixels in a landscape are not situated in the same patch (Jaeger 2000). $LD = 0$ when the landscape consists of a single patch and increases to one as patches become more maximally subdivided, (when every cell is a separate patch). The Landscape Division index is probably the most useful on its own as it can discriminate between a greater range of habitat patchiness in the landscape. These recommendations by Sleeman et al. (2005) have been used recently to document seagrass loss and fragmentation from a dataset spanning 71 years in Florida (USA), providing evidence that coastal developments have transformative impacts on vegetated habitats, with undetermined consequences for the provisioning of ecosystem goods and services (Santos et al. 2015).

## 9.4 Modelling Seagrass Seascape Processes

Spatially-explicit modelling is a very useful approach for investigating how interactions between organisms and their environment influences distribution of seascape classes, like seagrass patches and meadows. Such models can be used to describe processes as simple as linear relations between a couple of variables or as complex as projecting the interaction between different organisms and their environment over time (Pastor 2011). Despite the variety of modelling techniques currently available, all aim to simulate a process and its responses based on maximum simplicity, thus restricting the variables to only the ones that, are of interest or that produce greater effect while obtaining meaningful and realistic results. It is therefore imperative for any kind of modelling exercise to describe the capabilities and limitations of the simulations undertaken as well as their real use or application. The models can then add complexity depending on the number of variables as the input and the relations among these variables. The increase in computer power has allowed us to expand and assess more complex interactions, increasing the number of factors in the system while reducing the solving time.

Seagrass seascapes inhabit certain environments over a determined area, where the current environmental conditions are often used in models to define the suitable habitat or the fundamental niche. If biological factors such as competition are included in models, then the model represents the realised niche of an organism. The geographical expression of its realised niche at a particular time is the potential distribution of a species, denoting areas where there is fulfilment of both abiotic and biotic requirements (Soberón and Peterson 2005). Modelling suitable habitat for seagrasses aids in understanding contemporary seascape patterns, particularly in determining if gaps are edaphic in nature or a result of disturbance driven mortality (Bell et al. 1999). Understanding the evolution of seascapes however, depends on numerous factors affecting the system at different timescales.. Shifts can result from geological processes (millennia), cyclical events (decadal), rapid events (days) and lastly to biological responses within the organisms (minutes to seconds). It is therefore important to consider the timescale in question to properly address the processes influencing the dynamics of seagrass seascapes and the spatial extent and frequency at which responses are measurable or relevant (Zhang et al. 2013). Some of the major limitations on spatial modelling are the heterogeneity of the environment and our inability to work with the inherent complexity. Instead, we tend group all the spatial information into units that average information into a homogenous cell. The resolution of that spatial unit is a key factor when trying to explain specific processes. To properly address the dynamics of the environment to model, we need to determine the correct resolution and time-scale in order to work with the best amount of data with real implications for the time scale in question.

Spatially–explicit, individual-, or agent-based models, have been developed for research into seagrasses and the utilization of seagrass seascapes by mobile marine animals. These models simulate populations and communities by following individuals and their properties through space and time, taking into account attributes such as spatial location and physiological traits, behaviours and interactions among individuals (DeAngelis and Grimm 2014). As these models can incorporate any number of individual level mechanisms, they vary in their complexity and their purpose. For example, agent-based modelling and has been employed to assess fairy rings in sedges; a process of central dieback with regeneration within patches, and a structure recently observed in seagrasses (Wong et al. 2011). Agent-based models were also used to demonstrate that similar rates of horizontal and vertical rhizome growth in *Posidonia oceanica* was a source of the vertical structure in meadows in the Mediterranean, creating biotic reefs 1–3 m above the sediment (SWARM: Kendrick et al. 2005a). Spatial and temporal movement of drifting macro-algae was modelled to assess their influence on re-establishment of eelgrass in a Danish Fjord using an agent-based modelling framework (MIKE 3 FM ECOlab: Canal-Vergés et al. 2014). An individual-based model was used to explore the effect of seagrass fragmentation on the predator-prey relations of the blue crab, *Callinectes sapidus* (NETLOGO: Hovel and Regan 2008). Below, as an example of the value of landscape modelling, we describe in detail the application of an agent-based model that tests the nested hypotheses that clonal growth alone or clonal growth with recruitment from seeds could account for decadal changes in spatial arrangement in seagrass seascapes.

## 9.4.1 Case Study: Influence of Clonal Growth and Sexual Recruitment on Landscape Structure of Seagrass Assemblages

Seagrass ecosystems occur over broad spatial scales (seascapes) where they are characterised by a continuum from fragmented patches to continuous meadows. Seagrasses within these seascapes can contain one or multiple species of seagrasses with different rates of clonal growth and sexual recruitment. This study models the roles of clonal growth and sexual recruitment of *Posidonia* spp. and *Amphibolis griffithii* in accounting for changes in landscape fragmentation over decades.

Interactions between seagrass life-history processes and landscape patterns are complex, occur over large spatial and temporal scales and are difficult to explore through empirical experiments. Models of clonal growth (i.e. rhizome extension rates and branching angles) of different seagrass species have indicated that they influence spatial arrangement of seagrass patches (Marba and Duarte 1998; Sintes et al. 2005; Renton et al. 2011) and differences in clonal growth between seagrass species have been scaled-up to explain spatial patterns of seagrasses at seascape-levels (Vidondo et al. 1997; Bell et al. 1999; Kendrick et al. 1999, 2005a, b). Linking clonal growth and sexual recruitment to seascape-level patterns may be possible through the use of agent-based modelling techniques. In this study, we utilize the application of a spatially explicit, agent-based model, specifically developed to simulate clonal growth and sexual reproduction of seagrasses and other marine clonal organisms (seagrasses: Kendrick et al. 2005b; corals: Sleeman et al. 2005).

## 9.4.2 Methods

### 9.4.2.1 Study Region and Seagrass Assemblages

Maps of historical seagrass cover derived from geo-referenced aerial photography captured at a scale of 1:25,000 in 1972 and 1999 from the Success and Parmelia Bank regions, of Western Australia (32° 02′S, 115° 42′E: Fig. 9.5a and classified to species from towed video (see Kendrick et al. 2000 for methods). The 1972 and 1999 maps of seagrass distributions were saved as raster images with a 2 × 2 m-pixel resolution (Fig. 9.5b). Two seagrass genera, *Posidonia* spp. and

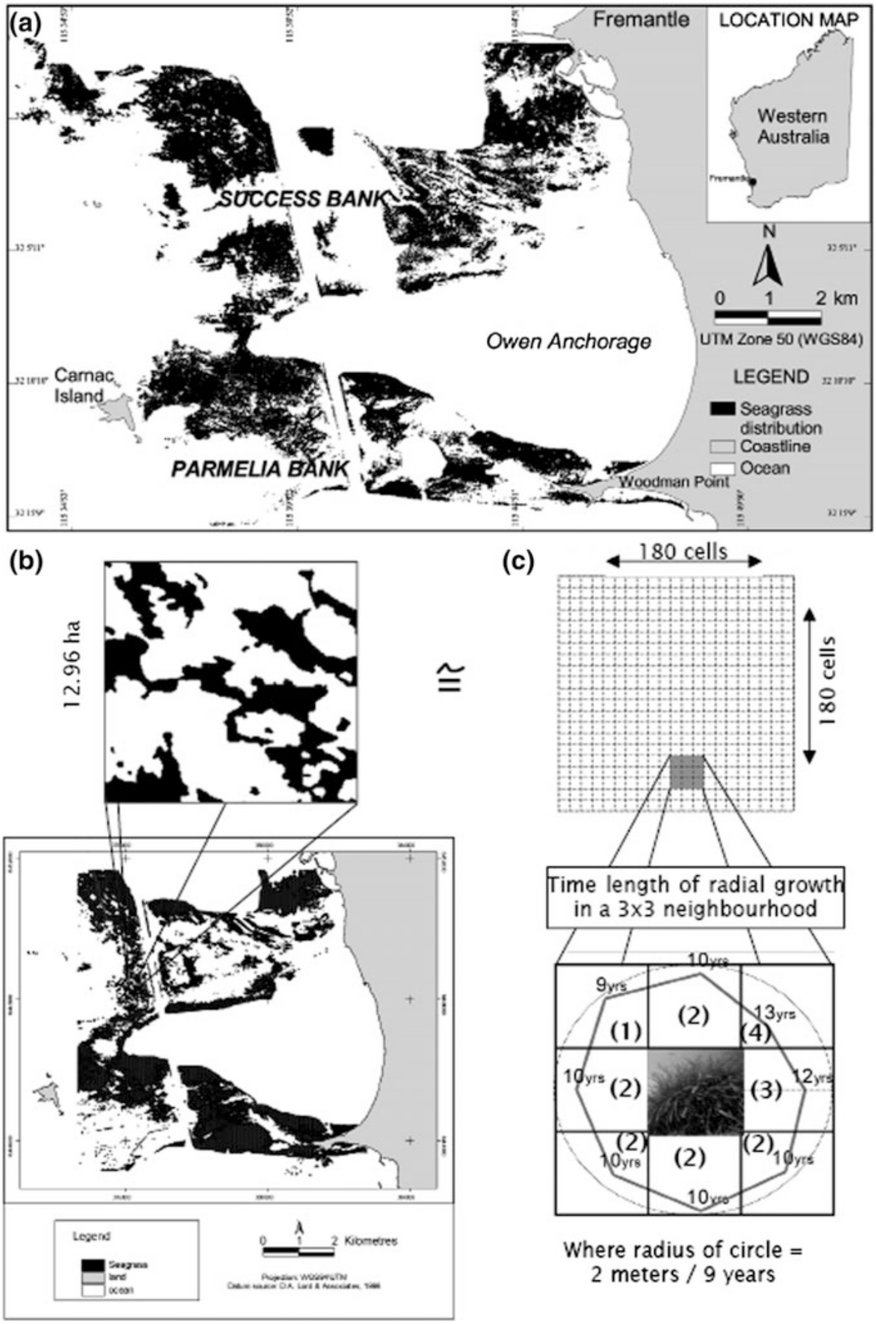

**Fig. 9.5** **a** On top, the study area in the South-west of Australia with the seagrass cover of 1972. **b** An example of a spactial unit consisting of 12.96 ha. **c** the grid of that spatial unit into cells of 4 m$^2$ and the assemblage Kernel of growth for the model, where the bold numbers in parenthesis represent the directional prioritation based on the study by Cambridge et al. (2002)

*Amphibolis grifithii,* covered much of the study area (Kendrick et al. 2000, 2008; Holmes et al. 2007) and were the focus for this modelling exercise (Fig. 9.5a).

#### 9.4.2.2 Analysing Changes in Fragmentation of Seagrass Assemblages Between 1972 and 1999

The 1972 and 1999 distribution maps for *Posidonia* spp. and *Amphibolis grifithii* were divided into 12.96-ha square regions (landscape units) (Fig. 9.5b). The resolution (grain) and size (extent) of the landscape units was representative of the size distribution of seagrass patches within the entire study area, where grain and extent were 2–5 times smaller and 2–5 times larger than the smallest and largest patch sizes, respectively (O'Neill et al. 1999). Only 12.96 ha units that exclusively contained either *Posidonia* spp. or *Amphibolis grifithii* in both 1972 and 1999 were extracted and used in the analysis.

#### 9.4.2.3 Modelling Clonal Growth and Clonal Growth with Sexual Recruitment of Seagrass Assemblages

Swarm is a spatially explicit, agent-based simulation model that was developed by researchers at the Santa Fe Institute as a tool to investigate spatial behaviour of interactive biological systems (Kreft et al. 1998; Luna and Stefannson 2000; Villa and Costanza 2000). In this study, Swarm was customized to specifically simulate clonal growth and sexual recruitment of seagrasses and details of the model can be found in Kendrick et al. (2005b). The seagrass model used in this study relies on the following assumptions: environmental conditions, such as nutrient availability, light and wave energy are considered to be uniform across the extent of the modelled space, and; the model is spatially unrestricted (modelled as a torus) such that boundaries do not inhibit growth.

The model adopts an agent-based approach whereby seagrasses are represented as a collection of units or agents within a grid (the species world), which interact via discrete events. The characteristics and behaviour of agents are defined by the implementation and interaction between three input files: (i) the assemblage kernel file, that determines the directional neighbourhood of clonal growth; (ii) the assemblage parameter file, that contains specific parameters including rhizome growth rate, life-span and sexual recruitment from the literature (Chap. 8), and; (iii) the initial map (specifying the starting location of the seagrass agents ($180 \times 180$ cells $\cong 2\ \text{m}^2$ pixels) Fig. 9.5b, c).

Patch growth data of *Posidonia australis* seagrass patches from Oyster Harbour (Cambridge et al. 2002), near Albany in Western Australia was utilised as a conservative standard from which the directional growth (kernel files) of both

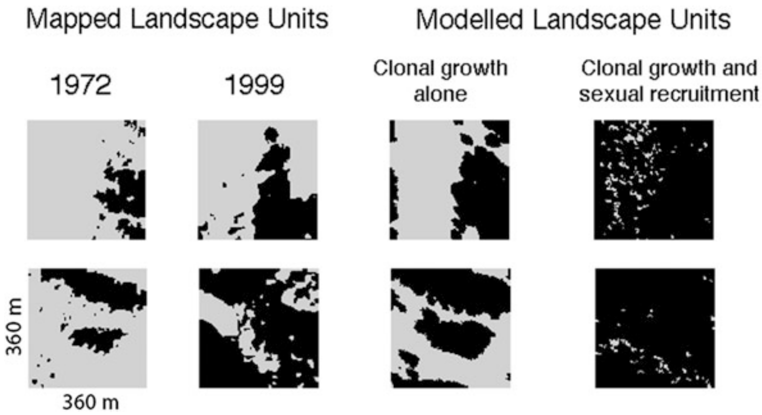

**Fig. 9.6** Each square represents a single landscape unit of 12.96 ha. (On the left) Evolution of two landscape units between 1972 and 1999. (Right) modelled outputs for the same units (1999), with and without sexual recruitment

*Amphibolis griffithii* and *Posidonia* spp. were defined. The average annual patch expansion in the eight cardinal directions was calculated from patch growth data and plotted in a compass rose diagram (Fig. 9.6c).

Rhizome growth rate in the model (growth probability factors) was the only parameter that was varied between the two genera and all other parameters were kept constant between both species. The growth probability factors for *Amphibolis griffithii* and *Posidonia* spp. were 0.22 and 0.11 or approximately 18 and 9 cm of radial growth per year, respectively.

The same parameter values for recruitment from seeds (seed probabilities, seedling survival, seedling interval, maximimum and minimum number of seeds per agent, and maximum number of seedlings allowed in the landscape) and minimum and maximum life span were used for both *Amphibolis griffithii* and *Posidonia* spp. There is little published information available for sexual recruitment of *Amphibolis griffithii* and *Posidonia* spp. (but see Rivers et al. 2011; Kendrick et al. 2017). Since seagrass seedlings occupy considerably smaller areas than 2 × 2 m patches (the minimum cell size), the seed interval was extended from once a year to once every 4 years, as it would take at least that amount of time before a cell could be partly occupied by a seedling growing between 6.5 and 19 cm per year. In addition to extending the seedling interval, the seed minimum and seed maximum values of individual agents was adjusted so that a single 2 × 2 m patch was only capable of producing either a single recruit (2 × 2 m patch) or no recruits. To ensure that recruitment did occur annually, the seed probabilities for the two assemblages were set at 0.9. The maximum number of seedlings allowed within the landscape at any one time step was set at 5,000 recruits or 6.5% of the total area (180 × 180 = 32,400 grid cells). Seedling survival for the first year was set as 1 in 10 (10%) to correspond with the high rates of recruitment mortality observed in the field (Kirkman 1998) although from unpublished recent studies this may be high.

*Posidonia australis* had a recorded rhizome lifespan (ranging between 8 and 18 years) this was applied as the minimum and maximum life-spans for both *Amphibolis griffithii* and *Posidonia* spp (Marba and Walker 1999) within the model.

Twenty landscape units from 1972 were selected randomly as the initial maps for each species. Clonal growth, with and without sexual recruitment, were modelled for each landscape unit for the 27 year period (1972–1999).

Following the completion of the modelling, the output maps were exported into a GIS and ran through the landscape indices software Fragstats 3.3 (McGarigal and Marks 1995) to calculate Area Weighted Mean Perimeter to Area Ratio, Landscape Division and total seagrass area, median patch area and number of patches. One-tailed paired t-tests were carried out to compare the differences between landscape structure among modelled outputs after 27 years (1972–1999) and measured structure from aerial photographs in 1999.

## *9.4.3 Results*

### 9.4.3.1 Comparing Model Outputs to Actual Seagrass Landscapes in 1999

Modelled reduction in fragmentation of *Amphibolis griffithii* and *Posidonia* spp. between 1972 and 1999 could be explained by clonal growth processes in the absence of sexual recruitment. Fragmentation for both modelled seagrass assemblages, measured as Landscape Division, was statistically significantly less than that observed in 1999 (Table 9.1 and Fig. 9.6).

### 9.4.3.2 *Amphibolis griffithii*

Modelling clonal growth alone produced similar spatial distributions to the actual observed spatial distributions of *Amphibolis griffithii* in 1999. Total seagrass area, median patch sizes, number of patches and seagrass fragmentation were not significantly different when comparing clonal growth from the model to the observed 1999 coverage (Table 9.1). The outputs produced from simulating 27 years of clonal growth and sexual recruitment for *Amphibolis griffithii*, had statistically significant less fragmentation (LD index) compared to observed distributions in 1999 (Table 9.1). Similar total seagrass areas, numbers of patches, median patch sizes, patch perimeter to area ratios (AWMPAR values) were observed between the model and 1999 aerial photographs.

**Table 9.1** Means, SEs and paired t-tests for change in seagrass cover in *Amphibolis griffithii* and *Posidonia* spp. patches and meadows measured as seagrass landscape indices between 1972 and 1999, measured from historical aerial photographs and modelled using the seagrass SWARM model

| | | Data type | | | | | | Comparison of observed and modelled | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Seagrass assemblage | Indices | Observed 1999 | | Modelled clonal growth alone | | Modelled clonal growth combined with sexual recruitment | | Modelled clonal growth alone | | Modelled clonal growth combined with sexual recruitment | |
| | | Mean | SE | Mean | SE | Mean | SE | Paired *t* statistic (n = 20, critical = 1.729) | P value (ns) | Paired *t* statistic (n = 20, critical = 1.729) | P value |
| Ag and Pc | Total seagrass area (hectares) | 8.02 | 0.91 | 6.72 | 0.89 | 10.39 | 0.96 | 1.19 | 0.25 | −1.73 | 0.099 (ns) |
| | Median patch area (hectares) | 4.85 | 1.28 | 2.66 | 1.01 | 8.60 | 1.33 | 1.31 | 0.207 | −2.06 | 0.054 (ns) |
| | Number of patches | 7.4 | 2.19 | 5.4 | 0.76 | 15.1 | 6.16 | 0.89 | 0.384 | −1.21 | 0.241 (ns) |
| | Area-weighted mean perimeter to area ratio | 0.77 | 0.18 | 0.70 | 0.13 | 0.88 | 0.26 | 0.30 | 0.769 | −0.32 | 0.756 (ns) |
| | Landscape Division | 0.54 | 0.08 | 0.69 | 0.08 | 0.28 | 0.09 | −1.84 | 0.081 | 2.39 | 0.027 (sig) |
| *Posidonia* spp. | Total seagrass area (hectares) | 6.94 | 0.88 | 6.50 | 0.93 | 8.47 | 1.06 | 0.77 | 0.450 | −2.27 | 0.035 (sig) |
| | Median patch area (hectares) | 1.86 | 1.01 | 1.20 | 0.82 | 1.60 | 0.91 | 1.08 | 0.294 | 0.85 | 0.406 (ns) |
| | Number of patches | 13.50 | 1.91 | 17.65 | 3.08 | 31.50 | 9.74 | −1.40 | 0.176 | −1.92 | 0.069 (ns) |
| | Area-weighted mean perimeter to area ratio | 1.32 | 0.22 | 1.75 | 0.30 | 1.67 | 0.37 | −1.81 | 0.085 | −1.17 | 0.257 (ns) |
| | Landscape division | 0.65 | 0.07 | 0.68 | 0.07 | 0.47 | 0.09 | −0.62 | 0.543 | 2.63 | 0.016 (sig) |

#### 9.4.3.3 *Posidonia* spp.

The spatial distribution (i.e. total seagrass area, median patch size, number of patches and fragmentation) produced by simulating clonal growth of *Posidonia* spp. was not significantly different from measured *Posidonia* landscapes in 1999 (Table 9.1). When clonal growth was combined with sexual recruitment, modelled landscape units had significantly greater total seagrass area and significantly lower Landscape Division (fragmentation) than observed from aerial photographs in 1999 (Table 9.1 and Fig. 9.6).

### *9.4.4 Discussion*

The most parsimonious interpretation from modelling is that clonal growth of seagrass patches and meadows existing in 1972 were responsible for the observed decrease in seagrass fragmentation and increase in seagrass cover between 1972 and 1999. Similarly, clonal growth was found to be the main mechanism for recolonisation and gap closure of seagrass meadows for *Cymodocea nodosa, Enhalus acoroides, Halodule wrightii, Syringodium filiforme, Thallassia hemprichii, Thallassia testudinum* and *Zostera caprocornii* (Duarte and Sand-Jensen 1990, Williams 1990, Duarte et al. 1997, Rasheed 1999, Rollon et al. 1998, Almela et al. 2008). Infilling and coalescence of seagrass patches increased when we included sexual recruitment in the agent-based model.

Faster rates of meadow cohesion in modelled *Amphibolis griffithii* was solely driven by faster rhizome spreading rates, as this was the only parameter we varied between taxa in the agent-based model. Horizontal rhizome growth rates of *Amphibolis griffithii* are 2–5 times faster (22.6 cm year-1: Marba and Duarte 1998, Marba and Walker 1999) than the *Posidonia* spp. (4–9.3 cm year$^{-1}$: Marba and Duarte 1998, Marba and Walker 1999).

Studies on *Posidonia australis*, *P. coriacea*, *P. sinuosa*, and *Amphibolis griffithi* have speculated that sexual reproduction has some importance in the recovery and maintenance of meadows, yet few studies have endeavoured to quantify this relative influence (Cambridge et al. 2002; Campey et al. 2002, 1999, 2000, 2012; Marba and Walker 1999) *Posidonia coriacea* contributes as little as 15 ± 3 seeds m$^{-2}$ year$^{-1}$ on Success Bank (Campey et al. 2002). Even if reproductive propagation appears to be occurring, seedling mortality is high, due to processes such as predation (Orth et al. 2006b and loss associated with storms and wave action (Kirkman 1998). Genetic studies of *Amphibolis* species in Western Australia suggest that sexual reproduction may be of limited importance to the maintenance of populations since they comprise few or single genotypes (Waycott et al. 1996).

In this modelling exercise we have not incorporated stochastic disturbance, and clonal growth and sexual recruitment are explored where disturbance through biological and physical mechanisms is a small-scale spatially random process expressed as mortality of the agents in the model (an agent is a 2 m × 2 m patch of seagrass). Persistent hydrodynamic disturbances such as wave forcing are known to affect patch and meadow configuration; examples for temperate Australia include linear bed forms in *Posidonia* spp. in Cockburn and Warnbro Sound and Rottnest Island, Western Australia (Marba and Duarte 1995; Cambridge 1999; Smith and Walker 2002; Kendrick et al. 2000). The influence of physical processes on the spatial configuration of seagrass landscapes has been considered in recent seascape modelling (Suykerbuyk et al. 2016) and is a valuable area of future research.

### *9.4.5 Conclusion*

In conclusion, agent-based modelling is a heuristic tool for developing hypotheses to test the links between seascape pattern and biological processes. In this case study the outputs from an agent-based model indicated that clonal growth alone appears to explain the increases in seagrass area (Kendrick et al. 2000) and cohesion of seagrass patches and meadows observed on Success and Parmelia Banks between 1972 and 1999. Also, increases in seagrass area and decreases in fragmentation of seagrass landscapes occur over decadal time scales for seagrass assemblages that exhibit slow rhizome growth. In our landscape simulation, this is a product of increases in size of seagrass patches resulting in coalescence into meadows.

## 9.5 Seagrass Seascapes and Faunal Community Structure and Abundance

This section reviews our present knowledge on the effects of seagrass lanscape patern on the fauna found in these shallow subtidal seascapes. The main messages from this research is that the importance of seagrass patchiness, patch size, leading edges and patch isolation in the distribution and abundance of faunal communities is highly variable in time and space and is highly species-specific (Bell et al. 2001; Connolly and Hindell 2006; Bostrom et al. 2006, 2010). Research in this area have suffered from experimental and sampling designs that confound effects of the landscape, habitat complexity, location, depth with time and spatial extent of sampling (Connolly and Hindell 2006). The species specific nature of responses to landscape pattern suggest an understanding of life history, dispersal and recruitment (Bostrom et al. 2010), behavior and predator-prey relations (Hovel and Regan 2008), and the matrix of landscape classes (e.g. seagrass species, reef and sand) within the seascape (Tanner 2006) are required for an effective landscape analysis. Species-specific studies have been the most effective in describing a landscape-organism relationship, for example between the blue crab (*Callinectes sapidus*) and eelgrass (*Zostera marina*) landscapes (Hovel and Lipcius 2001, 2002;

Hovel 2003) and assessing the feedbacks between the organism and the landscape (Hovel and Regan 2008; Mizerek et al. 2011).

The most common method of investigation into the effect of seagrass landscape continuity and fragmentation on faunal communities and populations was to divide the natural seagrass environment into broad categories. For example Fernández et al. (2005) investigated three seagrass patch classes around Capo Feto in the Mediterranean; continuous, large patches (diameter of 3–6 m) and small patches (diameter of 0.5–1.5 m) and found significant differences in the fish assemblage between fragmentation categories with higher species richness in fragmented beds versus continuous meadows. However, fish abundance remained the same across fragmentation classes with smaller individuals found in continuous beds. Interestingly the effect of fragmentation category was found to have a stronger influence on the fish assemblage than the effect of depth. Frost et al. (1999) examined the effects of two levels of seagrass heterogeneity, a continuous seagrass meadow versus a highly fragmented seagrass landscape, on infaunal macroinvertebrate abundance and diversity in Devon in the United Kingdom. Significant multivariate differences in infaunal macroinvertebrate abundances were detected, however, these could not solely be attributed to levels of fragmentation due to the confounding effect of location. Bowden et al. (2001) undertook a similar investigation comparing infaunal macroinvertebrate abundance and diversity in seagrass landscapes with two patch size categories, one comprising patches <10 m in diameter and one patches >30 m in diameter in the Isles of Scilly, south-west England. They reported a significant difference in the macroinvertebrate community structure between sites, patch sizes and in-patch location, and significantly more taxa in large patches than in small, however they did not control for seagrass area. Murphey and Fonseca (1995) in their comparison of low energy continuous seagrass landscapes with higher energy, patchy landscapes in Black Sound in North Carolina, found significantly more pink shrimp, *Penaeus duorarum*, in the continuous seagrass landscapes. They did control for differences in seagrass area but could not control for differences in location.

Ensuring that seagrass area and the effect of location is accounted for in analyses is a significant, yet common, problem encountered in research into fragmentation of seagrass using natural seagrass beds. One way to control for this is to use artificial seagrass units to create seagrass landscapes that may be manipulated to test for seagrass fragmentation while controlling for area, location and structural complexity. Healey and Hovel (2004) used artificial seagrass units in San Diego Bay, California to examine seagrass heterogeneity while experimentally controlling for seagrass area. Epifaunal abundance and diversity found to be highly variable among the continuous to highly patchy seagrass, among sampling periods and among individual species. However, for two out of three sampling dates, epifaunal diversity was highest and community composition was most dissimilar in patchy or very patchy beds, demonstrating that seagrass patch configuration influenced epifaunal communities independent of seagrass bed area or structural complexity, but was limited by the small scale of treatments where their extent was $\leq 1\ \mathrm{m}^2$.

### 9.5.1 *Faunal Studies Utilizing Landscape Metrics*

In Australia, New Zealand and SE Asia, we have led the way in studies that assess influences of seagrass seascapes on community structure, abundance and movement of seagrass associated fish and invertebrates (Table 9.2).

**Table 9.2** Summary of a selection of seagrass seascape studies that address landscape spatial pattern and faunal associations in Australia, New Zealand and South East Asia (1999–2015)

| Seascape scale | Variable | References |
|---|---|---|
| Landscape (10 s m to km) | Landscape continuity/heterogeneity | Salita et al. (2003) |
| | Patch | Pittman et al. (2004), Salita et al. (2003) |
| | Patch area | Connolly and Hindell (2006), Pittman et al. (2004), Salita et al. (2003), Turner et al. (1999) |
| | Patch isolation (nearest neighbour distance) | Connolly and Hindell (2006), Pittman et al. (2004), Turner et al. (1999) |
| | Patch shape (perimeter: area ratio patch fractal dimension) | Pittman et al. (2004), Salita et al. (2003), Turner et al. (1999) |
| | Adjacency (distance to adjacent habitats or geographic features) | Pittman et al. (2004), Skilleter et al. (2005) |
| | Edge | Connolly and Hindell (2006), Pittman et al. (2004), Statton et al. (2015), Vonk et al. (2010) |
| | Core | Pittman et al. (2004) |
| | Patch diversity | Pittman et al. (2004) |
| | Contagion (the probability measure of patch dispersion) | Pittman et al. (2004) |
| | Interspersion (a measure of the extent to which patch types are interspersed) | Pittman et al. (2004) |
| Classes (m to 10 s of m) | Patch size | Connolly and Hindell (2006), Jelbart et al. (2006), Pittman et al. (2004), Salita et al. (2003) |
| | Patch shape | Pittman et al. (2004) |
| | % seagrass cover | Turner et al. (1999) |
| | Edge effects (distance from seagrass-sand interface) | Jelbart et al. (2006), Pittman et al. (2004), Smith et al. (2011), Tanner (2005), Turner et al. (1999), Vonk et al. (2010) |
| | Number of halos (number of bare holes within a patch) | Salita et al. (2003) |
| | Nearest neighbour | Pittman et al. (2004) |
| | Interspersion | Pittman et al. (2004) |

### *9.5.2 Landscape Scale Indices*

Adjacency with other classes in the seascape, like mangroves or the mouth of estuaries, were found to be very important for fish and decapod crustaceans (Pittman et al. 2004; Skilleter et al. 2005). The adjacency of mangroves to seagrass meadows was positively related to fish and penaeid prawn abundances and more influential than density of seagrass meadows in Morton Bay.. Similarly, Hannan and Williams (1998) found distance from the mouth of an estuary in NSW was directly correlated to the toatl fish abundance within the estuary.

Generally, most faunal studies have tested correlations among fauna and multiple landscape indices. Pittman et al. (2004) tested patterns in fish and and decapod crustacean community structure and abundance against 15 landscape metrics representing 8 key metric categories: area, patch, edge, core, shape, nearest neighbour, diversity, contagion and interspersion, Similarly, Jackson et al. (2006) tested on fish communities a suit of 12 and Salita et al. (2003) six landscape indices. Those indices that were most influential included landscape composition, landscape heterogeneity (seagrass % cover, number of patches, average patch size, average perimeter:area ratio fractal dimension and the total number of halos within seagrass meadows), and landscape fragmentation (total edge, interspersion and juxtaposition of patches, patch richness and Shannon diversity) (Table 9.2). Interestingly, their results show that multiple landscape indices account for small to moderate amounts of percent variation, and that in combination rarely account for more than 65% of total variation in fish diversity and abundance.

### *9.5.3 Patch Scale Metrics*

A number of papers were found to link changes in seagrass associated fauna to patch scale and within patch scale variables, particularly those describing patch size, shape, % seagrass cover and edge effects (Table 9.2). Of these, most found that the responses were quite variable between species and through time and that patch metrics only explained small portions of faunal population or community response.

Strong relationships were found in some studies. For example, Pittman et al. (2004) found fish and penaeid prawn diversity and abundance declined abruptly when seagrass cover in meadows was less than 20% in Moreton Bay. Similarly, Turner et al. (1999) found a significant edge effect effect (within patch, leeward edge and windward edge) on benthic community composition in seagrass meadows in northern New Zealand. Similarly, edge effects were described for fish predation in Shark Bay (Statton et al. 2015) and fish abundance in Indonesia (Vonk et al. 2010).

### 9.5.4 Conclusion

The pattern of seagrass distribution and abundance in seagrass landscapes affects associated faunal populations and communities at the seascape, patch and within patch scale, but many of the significant interactions are location and taxon specific making generalizations difficult. Much of the present research has been correlative in nature and points to a need to understand both the specificity of scales in time and space for both the fauna and the seagrass within shallow subtidal seascapes. Hydrodynamic setting and adjacency of other major habitats have been shown to be important in determining faunal utilization of seagrass seascpaes and need further detailed investigation.

## 9.6 Summary

A seascape approach is essential to comprehend how the spatial properties of seagrass influence their growth and survivorship, as well as ecological interactions with other marine species e.g. the quality of nursery functions and fisheries productivity of seagrass ecosystems.. In Australia, we have traditionally focused on mapping extensive seagrass habitats and quantifying change in aerial extent, biomass and species composition. Through our extensive mapping efforts, we have been able to perform in depth analysis of spatial structure using landscape indices, which has revealed that no single index can be used to comprehensively quantifying the complex spatial aspects of seagrass seascapes. However, using a combination of Area Weighted Mean Perimeter to Area Ratio and Landscape Division indices provides a comprehensive assessment of spatial structure while avoiding strong correlation among indices. We are at the forefront of modelling landscape level changes, determining the underlying processes responsible for spatio-temporal patterns for some systems (e.g. Owen Anchorage, Moreton Bay). It is clear, however, that the spatial ecology of seagrass remains a critical area. Information on how growth patterns of rhizomes and patterns of seed recruitment contribute to the spatial heterogeneity of seagrass landscapes is sorely lacking, with only one example from Western Australia demonstrating the contribution of asexual and sexual recruitment to patterns in the seascape.

More effort needs to go towards combining remote sensing techniques with landscape ecology and conventional marine ecology, particularly in understanding the processes that influence the flow of energy and material across seascapes and the resulting patterns (Fig. 9.1). This can be achieved through studies of movement ecology, seascape genetics and meta-population modelling, where a combination of approaches will ultimately lead to a more integrating understanding of contemporary as well as evolutionary patterns in seagrass structure (Kendrick et al. 2017). Additionally, a better ecological understanding of the relationships between the indices used to quantify spatial structure and ecological processes must evolve.

Future research should specifically aim to clarify (1) The role of structural and functional connectivity at different spatial scales and (2) To what extent can refined indices improve the understanding of habitat connectivity for fisheries or marine zoning. One of the greatest challenges in marine conservation management remains the definition and establishment of habitat protection zones at appropriate scales for local, regional to biogeographic scales.

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# Chapter 10
# Seagrass Resistance to Light Deprivation: Implications for Resilience

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**Abstract** Seagrass habitat is strongly constrained by light availability. Decline in benthic light due to anthropogenic activities (e.g. eutrophication, dredging and catchment modification) is a major threat to seagrass ecosystems, both within Australia and internationally. Even in pristine conditions, light available to seagrasses can be highly variable on timescales ranging from seconds to years. This chapter outlines the three primary mechanisms which enable seagrass to adapt to and/or resist temporary light deprivation: (1) consumption of accumulated carbon;

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(2) reduction in rates of growth and carbon loss; and (3) increased efficiency of radiation capture and usage. The capacity to withstand severe light deprivation ranges from only two weeks for small, colonising seagrass species such as *Halophila ovalis*, to beyond two years for large, persistent species such as *Posidonia sinuosa*. This "tolerance time" depends on the magnitude and timing of the light deprivation, current environmental conditions (e.g. temperature and sediment sulphides) as well as preceding conditions. This chapter proposes a simple conceptual model for seagrass resilience to temporary light reduction, combining both resistance (the capacity of seagrass to survive the light deprivation event), and the capacity to recover once the disturbance ends. Data is synthesized for several potential indicators of seagrass resistance to light reduction.

## 10.1 Introduction

Light availability is a key determinant of seagrass distribution and habitat viability (Dennison 1987; Abal and Dennison 1996; Ralph et al. 2007). Like other plants, seagrasses require sufficient photosynthetically active radiation for photosynthesis and hence growth (Gallegos et al. 2009; Kahn and Durako 2009; Falkowski and Raven 2013; Baird et al. 2016). The light available to seagrass is affected by water depth, light attenuation coefficient of the water column, shading by epiphytes (Drake et al. 2003), optical properties and orientation of seagrass leaves (Zimmerman 2006) and macroalgal coverage (Hauxwell et al. 2001, 2003). Water clarity affects the lower depth limit of seagrass habitat (Duarte 1991a), and hence long-term decline in water quality is one of the major threats to seagrass ecosystems in Australia and worldwide, driven largely by catchment and coastal development (Walker 1992; Orth et al. 2006a; Grech et al. 2012).

Seagrasses predominantly absorb light in the blue (400–500 nm) and red regions (660–680 nm) of the spectrum (Fyfe 2003; Durako 2007). The total quanta and the spectral composition of light both change with depth (Kirk 2011). Within the water column, light is attenuated by suspended sediment, phytoplankton and coloured dissolved organic matter (CDOM) (Kirk 2011). Particulate material (including suspended sediments) attenuate shorter wavelengths (Baird et al. 2016), but the attenuation of light by suspended sediments is strongly affected by particle size (Van Duin et al. 2001). Attenuation of the blue-green region of the spectrum by CDOM greatly reduces the availability of light within the absorption peak of chlorophyll (Kirk 2011), while phytoplankton absorbs at similar wavelengths to seagrasses, at both ends of the spectrum (Van Duin et al. 2001; Ficek et al. 2004; Durako 2007). The effects of suspended sediments, phytoplankton and CDOM on the optical properties of water are so distinct that shifts in reflectance spectra can be detected using remote sensing (Blondeau-Patissier et al. 2014; Devlin et al. 2015), and thus the risk to benthic habitats such as seagrasses from declining water quality can be assessed remotely (e.g. Petus et al. 2014). Due to selective absorption across the spectrum caused by suspended sediments, phytoplankton and CDOM, using a single light attenuation coefficient, $K_d$, may underestimate the light available for photosynthesis (Moore et al. 1997). Photosynthetically usable radiation (PUR) weights the availability of quanta at specific wavelengths to the efficiency with which they are absorbed (Morel 1978); however when attenuation coefficients based on PUR and PAR were compared, they were virtually indistinguishable within three seagrass meadows in the Western Atlantic (Gallegos et al. 2009). To date, there has been little research on the impact of changing light quality on photosynthetic rates in Australian seagrasses.

Numerous anthropogenic activities can affect the quantity and quality of light available to seagrass, through increasing concentrations of suspended sediment, phytoplankton, and CDOM, and promoting epiphyte and macrophyte growth (Walker and McComb 1992; Ralph et al. 2006; Kirk 2011). Nutrient enrichment (i.e. eutrophication) is commonly an unintended consequence of coastal development and catchment modification, and contributes to water column chlorophyll (Duarte 1995; Webster and Harris 2004), macroalgal blooms and excessive epiphytic coverage on seagrass leaves (Cambridge et al. 1986; Frankovich and Fourqurean 1997; Lee et al. 2007). For example, in Cockburn Sound, near Perth in Western Australia, extensive seagrass loss in the 1960s and 1970s was attributed to heavy epiphyte growth caused by industrial effluent rich in nutrients (Cambridge et al. 1986). Light reduction associated with turbidity plumes can also threaten seagrass. For example, light attenuation can be increased by dredging (Erftemeijer et al. 2006; McMahon et al. 2011), flood plumes (Collier et al. 2012a; Petus et al. 2014), and sediment resuspension may be further enhanced following seagrass loss (Moore 2004; van der Heide et al. 2007). There are some notable successes in managing and minimising potential impacts to benthic light and hence seagrass abundance and distribution, particularly for acute localised dredging (e.g. Chartrand et al. 2016). However in general, ongoing declines in water quality and reductions in light availability continue to place localised pressure on seagrass meadows (Wooldridge 2016). Light limitation adds to other water quality stresses such as herbicides (Negri et al. 2015), salinity (Hillman et al. 1995), disease prevalence, thermal stress (Collier et al. 2016), and physical stress (Walker et al. 1989) to contribute to the global crisis for seagrass meadows (Waycott et al. 2009). Furthermore, sea-level rise due to climate change will increase water depth, reducing benthic light availability and habitat suitability for seagrass (Saunders et al. 2013).

While most seagrass species have relatively high light requirements (Dennison et al. 1993; Duarte 1995), these angiosperms are widely distributed in dynamic coastal estuaries and habitats, subject to variable benthic light conditions. To illustrate, the variability of light over daily, monthly and annual time scales in an Australian coastal embayment is shown in Fig. 10.1. Cloud cover can reduce incident and hence benthic light on timescales ranging from a few seconds or minutes (Fig. 10.1a), through to days (Fig. 10.1b) or even weeks (Longstaff et al. 1999). Benthic light is also affected by interaction between diurnal cycles of sun, tides and wind. Interactions between daily light and tide cycles will have greatest

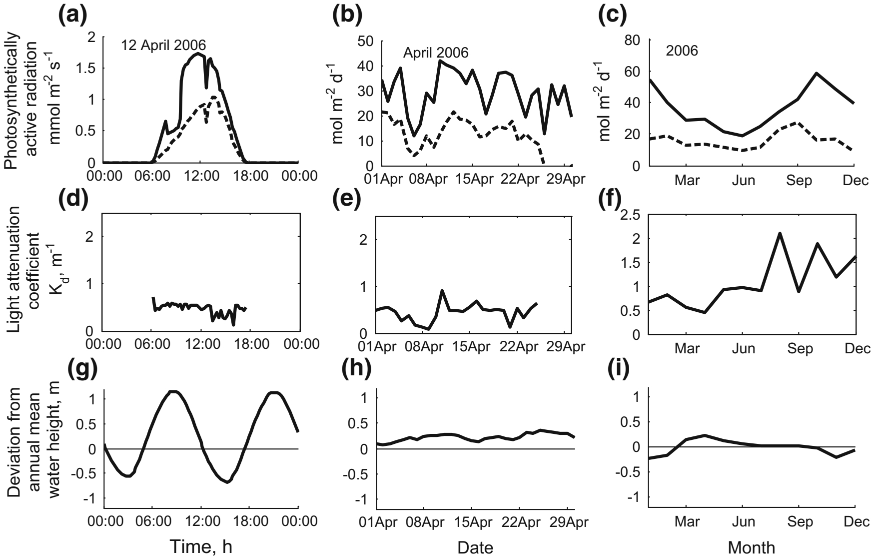


**Fig. 10.1** Daily, monthly and seasonal variations in **a**–**c** incident light (solid line) and light 0.74 m above sediment (dashed line), **d**–**f** light attenuation coefficient, and **g**–**i** water depth deviation from annual mean depth. Measured on the Eastern Banks of Moreton Bay, SE Queensland, Australia during 2006 (Maxwell et al. 2007)

impact on seagrass light conditions where: (1) daily tide causes large variability in benthic light (e.g. due to large tidal range and/or low water clarity); (2) tidal progression is slow, e.g. low tide occurs at the same time of day for weeks or even months; and/or (3) daily variation in light attenuation is large, e.g. sediment resuspension associated with tidal currents or diurnal wind patterns. To illustrate these interactions, in Fig. 10.1 maximum incident light on 12 April 2006 occurred at 11:45 am (Fig. 10.1a, solid line), light attenuation declined at 1:30 pm (Fig. 10.1d), and minimum depth (low tide) was at 3:15 pm (Fig. 10.1g). As a result, highest benthic light occurred at 3:15 pm (Fig. 10.1a).

Over seasonal timescales, light available to seagrasses is affected by variations in incident light dose, water clarity, and longer-term tidal cycles. Seasonal changes to rainfall and runoff can affect water quality. Furthermore, warmer waters in summer can promote phytoplankton growth, reducing water clarity (Dennison and Abal 1999). Seasonal changes to local weather patterns can affect wind speed and direction, and hence sediment resuspension (Kehoe et al. 2012). An example of competing seasonal influences on local benthic light conditions is illustrated in Fig. 10.1c, where the mean daily incident light dose varies from less than 20 mol m$^{-2}$ d$^{-1}$ in austral winter to a peak of almost 60 mol m$^{-2}$ d$^{-1}$ in the austral summer on the Eastern Banks in Moreton Bay, SE Queensland, Australia. During summer periods, increased precipitation and subsequent runoff diminish water clarity (Dennison and Abal 1999), but there is limited variation in tidal range at the seasonal time scale (Fig. 10.1i). Since incident light and light attenuation are both highest in summer at this location, maximum benthic light dose occurs in the austral spring (Fig. 10.1c).

On longer timescales, flood-dominated and drought-dominated climate cycles can generate both short-term and long-term variability in light. For example, in January 2011 a major flood caused an extensive turbidity plume in Moreton Bay, which decreased light available to seagrasses for approximately 6 months (O'Brien et al. 2012). The flood was caused by a one in 50 year rainfall event, which arose from interactions between two climate cycles: the El Niño-Southern Ocean oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). Large floods and cyclones also contributed to decline in seagrass area of 84% and biomass reduction of 99% over a 5-year period from 2007 to 2011 further north along the Queensland coast in Cleveland Bay, part of the Great Barrier Reef (Petus et al. 2014). Annual seagrass loss was highly correlated to turbidity plume exposure during the monsoon season. In this case, repeat or chronic exposure to acute short-term events drove the loss of seagrasses.

The impacts of acute and chronic light reduction on seagrass depends on interactions between anthropogenic processes driving light decline, natural variability in light conditions, and the mechanisms by which seagrasses respond to changes in light. Seagrass loss will occur if long-term light availability falls below minimum seagrass light requirements (Duarte 1991b; Dennison et al. 1993; Collier et al. 2012a). More difficult to predict is the impact of temporary or intermittent light reduction, which depends on species characteristics (Longstaff and Dennison 1999; Longstaff et al. 1999; Collier et al. 2016), duration and severity of light deprivation (Lavery et al. 2009; Collier et al. 2016), light history (Maxwell et al. 2014), and other environmental factors such as season (Chartrand et al. 2016), water temperature (Collier et al. 2016), and sediment characteristics (Enríquez et al. 2001; Brodersen et al. 2015).

This chapter outlines the mechanisms controlling the resistance of Australian seagrass to light deprivation, which we define as the capacity of seagrass plants and communities to adapt to and withstand chronic or acute light deprivation, such that some live biomass survives. We also outline how species characteristics, duration and severity of the light decline, preceding light conditions and other environmental conditions affect the seagrass resistance to light decline, and discuss the implications for resilience.

## 10.2 Eutrophication and Seagrass Light Availability

Anthropogenic eutrophication has resulted in seagrass loss worldwide due in large part to fundamental changes in light climates (Burkholder et al. 2007). Increases in nutrient loadings tend to favour biomass accumulation of fast growing phytoplankton, epiphytic algae, and free floating macroalgae, all of which can directly attenuate and alter the quality of light reaching seagrass canopies

(Hauxwell et al. 2001, 2003). Meadow response to decreased light from nutrient enrichment in Maryland and Virginia, U.S. showed a change as nutrient loading increased from healthy meadows, to meadows with epiphytes on them, to meadows with heavy macroalgal epiphyte loads, to seagrass loss and macroalgal survival, and ultimately only phytoplankton survival (Wazniak et al. 2007). Epiphytes can reduce light penetration to seagrass leaves by almost two thirds at peak chlorophyll absorption wavelengths (Silberstein et al. 1986; Drake et al. 2003). Water residence times, hydrodynamics and geomorphology can all influence the expression of eutrophication (Ferguson et al. 2017). For example, in the relatively deep Cockburn Sound WA, nutrient-rich industrial effluent stimulated epiphyte growth in near shore *Posidonia australis* meadows (Silberstein et al. 1986; Cambridge et al. 2007), resulting in competition for light between seagrass and epiphytes and widespread seagrass loss of this slow growing species due to light limitation (Cambridge et al. 1986).

The mechanisms underlying the loss of seagrass due to eutrophication vary, and do not always arise simply from reduced photosynthesis rates as may be expected. Numerous studies have shown that reduced light interacts with other impacts of eutrophication to cause seagrass loss. For example, while reductions in available light due to shading by *Ulva* were found to have no impact on photosynthetic performance of *Zostera marina*, large increases in pH associated with *Ulva* growth interacted with reduction in light to cause stress (Mvungi et al. 2012). Large accumulations of macroalgae biomass associated with eutrophication can cause increased sulphide exposure in the rhizosphere resulting in an increase in the minimum light requirements of *Zostera* spp. (Kenworthy et al. 2014; Ferguson et al. 2016), thereby amplifying the effects of increased light attenuation. Remineralisation of detrital algae biomass can also result in localised high concentrations of ammonium which may reach toxic levels for seagrass in poorly flushed areas (Van Katwijk et al. 1997). Loss of seagrasses due to the mechanisms described above may increase sediment resuspension in denuded areas, thereby further reducing water clarity and accelerating additional seagrass loss (Maxwell et al. 2017).

The relative abundance and succession of seagrasses and algal groups in response to increasing cultural eutrophication (and hence their impact on light climate) is usually complex (Cambridge et al. 2007), yet general patterns are evident. In the Virgin Islands in the Caribbean, plant recolonization of denuded plots showed that early successional stages for seagrass meadows include rhizophytic algae and fast growing seagrass pioneer species such as *Halodule wrightii* and/or *Syringodium filiforme*, followed by climax species such as *Thalassia testudinum*, a species which is larger and grows slowly and its further presence leads to the diminishment of the earlier species (Wazniak et al. 2007). These successional stages can also be seen inversely form meadow degradation, for example in Florida in the USA, long term nutrient enrichment experiments shifted the seagrass community structure from the climatic *T. testudinum* to the pioneer *H. wrightii* (Fourqurean et al. 1995). Succession linked to eutrophication can also be broadly described according to system morphology: shallow systems tend toward macroalgae dominance; while in deeper systems macroalgae and epiphytes are initially stimulated but phytoplankton ultimately dominates at highest loadings (Burkholder et al. 2007).

## 10.3 Seagrass Survival During Light Deprivation

The long-term survival of seagrasses in reduced light conditions will depend on whether a positive carbon balance can be maintained (Ralph et al. 2007). In periods of light deprivation the capacity of seagrasses to produce carbon through photosynthesis is compromised. This light reduction can lead to a carbon deficit, where the carbon needed to sustain the living biomass is greater than production, as shown by the carbon balance in Fig. 10.2. Seagrasses can survive substantial periods of carbon deficit utilizing stored non-structural carbon accumulated (primarily in the rhizomes) during periods of net positive production (Gordon et al. 1994; Alcoverro et al. 2001; Collier et al. 2009; Lavery et al. 2009). Under light deprivation, the resistance capacity of the seagrass (and hence survival period) can be extended if carbon consumption declines, e.g. through reduced growth rate and/or the respiratory burden (Brun et al. 2003; Ralph et al. 2007; Collier and Waycott 2009). Seagrass photosynthesis rates can also be enhanced under low light conditions by

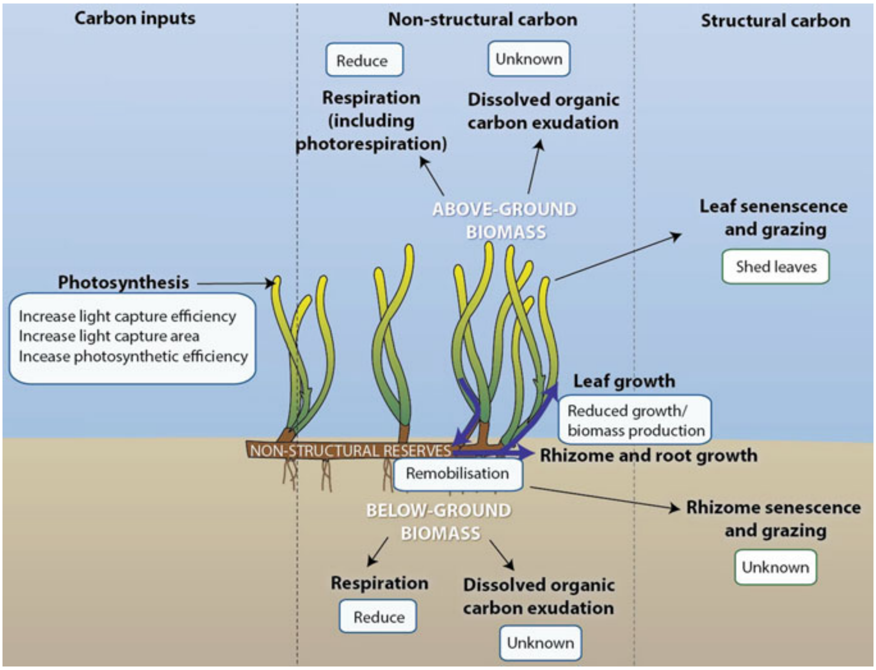


**Fig. 10.2** Conceptual model of seagrass carbon budget, including responses to light deprivation

increased efficiency of radiation capture and conversion (Carruthers and Walker 1997), greater photosynthetic efficiency within leaves and/or intercepting a higher proportion of light (Ralph et al. 2007; Collier et al. 2009). Carbon can also be lost through exudation (Fig. 10.2), but this typically has a minor impact on the overall budget and does not appear to be affected by light reduction (Kaldy 2012).

Therefore there are three key mechanisms that underpin seagrass resistance to light deprivation: utilization of stored carbon, reduction in carbon consumption through reduced growth and respiratory burden, and increase in the efficiencies of photosynthesis and light capture. Each of these mechanisms is outlined in more detail in the following subsections.

### 10.3.1 Accumulated Carbon Can Offset Impacts of Light Reduction

Carbon fixed by the plant is either allocated to structural components (e.g. cell walls, leaf, rhizome and root structures), or is stored as non-structural carbon (e.g. sugars and starches) which can be remobilised to supply carbohydrate for respiration and other processes (Fig. 10.2). This occurs over the daily light cycle: carbon fixed during the day fuels respiration during the dark hours (Rheuban et al. 2014). Time-scales of storage and remobilisation can vary for different forms and locations of non-structural carbohydrates. For example, longer term relief from light stress is typically provided by carbohydrates (sugars or starch, depending on the species) stored in the rhizomes (Longstaff et al. 1999; Ralph et al. 2007; Collier et al. 2009; Lavery et al. 2009). There is very little evidence that leaves play an important role for long-term storage, but the total non-structural carbohydrate content of leaves may provide resistance to very short-term light reduction.

In highly seasonal conditions, seagrass can survive long periods of negative carbon budgets, so long as the overall carbon budget is positive over the annual growth cycle (Dennison 1987; Burke et al. 1996). For example, *Posidonia oceanica*, the dominant seagrass in the Mediterranean, maintains a positive carbon balance for as little as 2 months of the year (Alcoverro et al. 2001). For the remaining 10 months, reserves of non-structural carbon are consumed by growth and loss processes (Alcoverro et al. 2001). Like *P. oceanica*, carbon reserves of the Australian seagrass *Posidonia sinuosa* can support plant requirements over very long time periods, and thus this species can persist for up to two years in almost complete shading (Gordon et al. 1994; Collier et al. 2009).

The timing of light deprivation will affect non-structural carbon reserves, and therefore affect the ability of seagrasses to resist light deprivation, particularly if carbon reserves are strongly seasonal (Alcoverro et al. 2001; Lavery et al. 2009), or if the recurrence time of multiple light deprivation events is less than the time needed for full recovery of carbon reserves (Gordon et al. 1994; Duarte 1995; Collier et al. 2009).

Accumulated carbon enables the large, slow-growing seagrasses, such as *Posidonia* spp. and *Thalassia* spp., to persist even in suboptimal light conditions. However the high biomass and slow growth rates which contribute to the high resistance of persistent species also mean that recovery can be very slow (Gordon et al. 1994; Erftemeijer et al. 2006; Collier et al. 2009; Unsworth et al. 2015). Orth et al. (2006a) and Kilminster et al. (2015) classified seagrass genera on a spectrum ranging from small, fast-growing colonising (or ephemeral) genera which have low resistance and high recovery capacity, through to large, slow-growing persistent genera with high resistance and low recovery. Opportunistic seagrasses fall in between these two extremes, with moderate capacity for both resistance and recovery (O'Brien et al. 2017).

While there is some overlap between these three classes (persistent, opportunistic, and colonising), this classification system is consistent with the tolerance to light deprivation observed for seven Australian seagrass species (Table 10.1). We define "tolerance time" as the duration of light deprivation which can be tolerated

**Table 10.1** Australian seagrass tolerance to long-term light deprivation

| Species | Life history classification | Time to complete loss | Shading | Reference |
|---|---|---|---|---|
| *Halophila ovalis* | Colonising | 38 days<br>2*, 6$^{\#}$ weeks | >99%<br>100% | Longstaff and Dennison (1999)<br>Collier et al. (2016) |
| *Halodule uninervis* | Colonising/ opportunistic | 119 days<br>15*, 20$^{\#}$ weeks<br>100 days | 99%<br>100%<br>>99% | Collier et al. (2011)<br>Collier et al. (2016) (predicted)<br>Longstaff and Dennison (1999) |
| *Zostera muelleri* | Colonising/ opportunistic | 76 days<br>4*, 8$^{\#}$ weeks | 99%<br>100% | Collier et al. (2011)<br>Collier et al. (2016) |
| *Cymodocea serrulata* | Opportunistic | 100 days<br>11* weeks<br>19$^{\#}$ weeks | 99%<br>100%<br>100% | Collier et al. (2011)<br>Collier et al. (2016)<br>Collier et al. (2016) (predicted) |
| *Thalassia hemprichii* | Persistent | 133 days | 99% | Collier et al. (2011) |
| *Amphibolis griffithii* | Persistent | 9 months | 90–92% | Lavery et al. (2009) |
| *Posidonia sinuosa* | Persistent | 2 years | 98% | Collier et al. (2009) (predicted) |

Life history classifications are according to Kilminster et al. (2015) *27.7 °C, $^{\#}$22.7 °C before plant death, it is therefore a good proxy for resistance to light reduction. While tolerance time depends on a range of factors, including the magnitude of light reduction, temperature and other environmental conditions, observed tolerance times are lowest for colonising seagrass and highest for persistent species (Table 10.1).

### *10.3.2 Reducing Growth and Carbon Loss Rate Can Offset Impacts of Light Reduction*

When carbon fixation rates decline due to light deprivation, cellular maintenance and growth will gradually consume carbon reserves, unless the decline in production is offset by reduced growth and respiration (Collier et al. 2012b). Where light reduction is sufficiently mild, reductions in growth rate and/or respiratory burden may be enough to rebalance the carbon budget. For example, under moderate shading (12–39% reduction), soluble sugars contained within rhizomes of *P. sinuosa* were consumed in the first 105 days of shading (Collier et al. 2009). Following plant-scale modifications, including reduction in respiratory burden through shoot loss, the carbohydrate content and leaf growth rates returned to control levels (between 150 and 200 days) despite the shading treatment remaining in place.

Responses at scales ranging from biochemical/metabolic to morphological/plant-scale can reduce the respiratory burden of maintaining cellular processes, such as ATP formation, biosynthesis, photorespiration and the regulation of cellular redox (van Dongen et al. 2011). Due to a lack of studies on these processes in seagrasses, the effects of reduced light levels on these biochemical pathways cannot be explored in detail.

Plant-scale processes can reduce the amount of seagrass biomass requiring cellular maintenance, and hence reduce the rate at which carbon reserves are consumed during times of net negative carbon production. For example, canopy thinning (Collier et al. 2011) is one of the earliest detectable morphological changes of light stress, and can occur within 2 weeks of severe light deprivation (Collier et al. 2012b). The oldest leaves are rapidly dropped from shoots, thereby reducing leaves per shoot (or leaves per cluster for *Amphibolis* species). Leaves have the highest respiratory demand per unit biomass of all plant parts: respiration rates were 4–7 times higher in leaves than roots/rhizomes for *P. sinuosa* and *P. australis* (Masini et al. 1995). Epiphyte coverage can reduce light penetration to seagrass blades (Brush et al. 2002), and thus the loss of older leaves, with potentially higher epiphyte coverage than younger leaves, may have additional benefits for light availability. Hence leaf loss is a quick and efficient method for reducing carbon debt. Loss of older leaves increases the efficiency of plant-scale carbon utilization because older leaves have lower rates of photosynthesis (Alcoverro et al. 1998).

In meadows with complex canopy structure, the loss of leaves may not be uniform, but typically occurs in the central part of the canopy where biomass density is greatest (Mackey et al. 2007; McMahon and Lavery 2014). This is likely to be a particularly useful strategy for coping with short-term and temporary light deprivation, as the plant can continue to grow and replace lost leaves after light conditions improve (McMahon and Lavery 2014). However there can be trade-offs between reducing respiratory burden and maximising photosynthetic light capture.

Whole shoots can also be shed to reduce respiratory carbon loss (Lavery et al. 2009; McMahon and Lavery 2014), and the consequent canopy thinning also has benefits for radiation use efficiency, as outlined in the following section. Shoot loss tends to occur after leaf shedding, on timescales of weeks to months (Collier et al. 2016). Shoot loss in *Halophila* species is functionally equivalent to leaf loss in other species, and happens over a similar time frame of weeks to months (Longstaff et al. 1999).

Changes in below-ground biomass are harder to measure, particularly using repeated studies, as sampling methods are destructive. While it is clearly demonstrated that light deprivation can reduce rhizome biomass (Abal et al. 1994; Longstaff et al. 1999; Collier et al. 2011), the underlying processes associated with this loss are not known. For example, do older rhizome parts senesce analogous with leaf loss, or is there a reduced production of new rhizome, and at what time scale do changes occur?

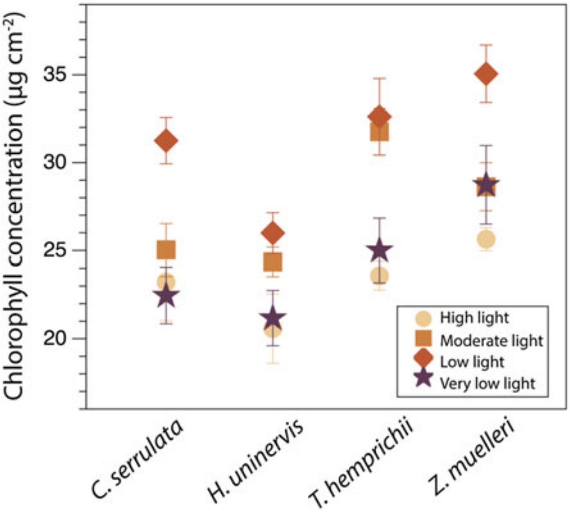
## *10.3.3 Resistance Enhanced by Efficiency of Radiation Capture and Use*

In seagrasses, while carbon reserves can be drawn on to survive light deprivation of finite duration, plants also have the capacity to adapt to reduced light. If the light reduction is not too severe, increased rate of carbon fixation per unit of biomass can balance the seagrass carbon budget. There are two key mechanisms by which carbon fixation per unit biomass can increase (1) improvements to photosynthetic efficiency through in-leaf processes (such as elevated chlorophyll content and/or change to pigment ratios) and (2) increased light capture per unit biomass through leaf modifications (e.g. elimination of self-shading through biomass reduction and/or changes in leaf shape and size).

### 10.3.3.1 Improved Photosynthetic Efficiency

Photosynthetic rates can change rapidly in response to changing light conditions. Commonly observed responses to light decline include elevated total chlorophyll

**Fig. 10.3** Concentration of chlorophyll a in leaves of four species of tropical seagrass after 15 days under four light treatments in aquaria: very low (99% shading), low (86% shading), moderate (69% shading) and high light (33% shading). Redrawn from (Collier et al. 2012b)



content to maximise light capture (Fig. 10.3), decreased ratio of chlorophyll a to b to improve light absorbance efficiency, and changes to efficiency of within cell photosynthesis (Waycott et al. 2005; Larkum et al. 2006a; Ralph et al. 2007). However, seagrasses can have limited capacity to improve light capture through gains in pigment concentration, as their chlorophyll is constrained to the epidermal layer (Enríquez et al. 2002; Ralph et al. 2007).

While light deprivation is known to affect the concentration of essential photosynthetic pigments, the direction of the effect is inconsistent between species. A meta-analysis of 58 studies by McMahon et al. (2013) showed variable response for both chlorophyll concentration and the ratio of chlorophyll a:b; thereby suggesting that the widely held paradigm of chlorophyll response to shading may not be as simple as suggested. For some species, shaded leaves typically have higher chlorophyll concentration than unshaded leaves e.g. *Amphibolis griffithii* (Mackey et al. 2007), *P. sinuosa* (Collier et al. 2007), *Zostera capricorni* (Abal et al. 1994), *Halodule pinifolia* (Longstaff et al. 1999). However in smaller, faster growing species like *H. ovalis,* chlorophyll concentration decreased following light deprivation (Longstaff and Dennison 1999).

While improved photosynthetic efficiency can enhance seagrass resistance to light deprivation, there are limits to photoadaptation. For example, in a progression of shading treatments ranging from high to very low light (Fig. 10.3), chlorophyll concentrations increased at moderate and low light intensities, but not under very low light.

The complexity of photoacclimation processes means that changes in seagrass photosynthetic efficiency in response to light conditions can be difficult to predict or evaluate. Changes in increased saturating irradiance and decreased electron transfer rate in response to light deprivation is fairly consistent amongst most studies and most species (McMahon et al. 2013). For many photosynthetic parameters, however, the effects of light reduction are unclear or inconsistent (Longstaff and Dennison 1999; Longstaff et al. 1999; Collier et al. 2007; McMahon et al. 2013), and may also depend on intensity and duration of light reduction, species characteristics, light history and environmental conditions. For example, temperature (Campbell et al. 2006) and herbicides (Negri et al. 2015) can induce photokinetic responses in seagrass, which can reduce the ability of plants to acclimate or adapt to light reductions, and hence affect the resistance of seagrass to light deprivation.

### 10.3.3.2 Leaf and Canopy Architecture

Self-shading can strongly modify the light environment within the seagrass canopy (Enríquez et al. 2002; Zimmerman 2003; Hedley et al. 2014). When benthic light is reduced, leaf biomass and leaf area index LAI (the area of seagrass leaves per unit ground area, i.e. leaf $m^2$/ground $m^2$) also typically decline (e.g. Fig. 10.4a), reducing self-shading (Duarte 1991b; Enríquez and Pantoja-Reyes 2005). For example, reduction in leaves in the mid-canopy (where the maximum leaf biomass is located) was an observed response of *Amphibolis griffithii* to light deprivation (McMahon and Lavery 2014). In combination with reduced leaf number and LAI, leaf length of remaining leaves typically increases in response to shading, which increases both the photosynthetic area, and the proportion of the leaf higher in the

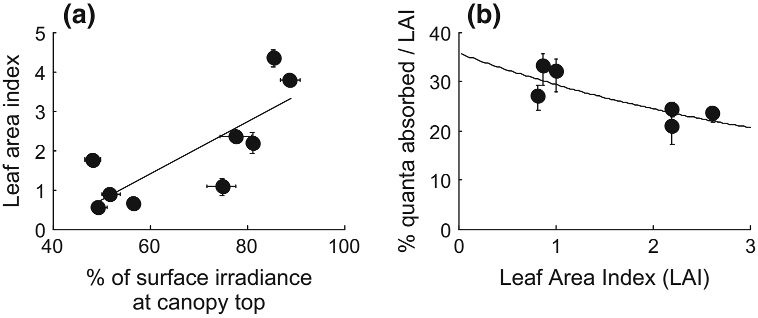


**Fig. 10.4** **a** Leaf area index (LAI) decreases with decreasing light availability (reproduced from Enríquez and Pantoja-Reyes 2005, Fig. 4a), **b** proportion of light absorbed per LAI increases as LAI declines (modified from Hedley and Enríquez 2010, Fig. 10; data extracted using the program xyExtract)

water column, where potentially higher irradiance is available. These morphological responses increase the absorption of light per unit leaf area (Fig. 10.4b), and ultimately improves the potential for seagrass to tolerate the impact of light deprivation. As for in-leaf processes, however, there are limits to how much changes in leaf and canopy architecture can offset light reduction.

## 10.4 Seagrass Response to Light Reduction: Implications for Resilience

The mechanisms outlined above ultimately affect tolerance time, the maximum duration of light deprivation which seagrass can survive. If the disturbance to light conditions exceeds the seagrass resistance capacity (i.e. if duration of light diminishment is longer than the tolerance time), then plant death, changes in species composition, or meadow loss will occur. If the meadow also lacks recovery features such as seed banks, or access to new propagules through connected systems, then recovery may not be possible until a source is introduced.

Where there are strong feedbacks between seagrass and environmental conditions (e.g. sediment resuspension or water column nutrients), seagrass absence can result in a change in state such that conditions become unsuitable for recolonisation (Nyström et al. 2012; Maxwell et al. 2017). Thus seagrass loss can be difficult or impossible to reverse in many cases (van Katwijk et al. 2009, 2016). Protecting and enhancing seagrass ecosystem resilience is important for avoiding change in state to degraded conditions (Suding et al. 2004; Connelly et al. 2018), where resilience is the capacity to adapt and transform in response to disturbance without losing key ecosystem structure and function (Levin et al. 2012). Resilience is a function of both resistance and recovery (Erftemeijer et al. 2006; Unsworth et al. 2015; O'Brien et al. 2017), as explained in Fig. 10.5.

### *10.4.1 Environmental Conditions Affect Tolerance Time*

Tolerance time depends on environmental conditions, including temperature, species characteristics and magnitude of light deprivation, as shown for four species of Great Barrier Reef seagrasses in Fig. 10.6. While seagrass can typically survive longer when light deprivation is less severe, tolerance time varies both within and between species (Fig. 10.6).

Tolerance time is likely to decline when respiration demand is increased by environmental conditions, such as higher temperatures (Collier et al. 2016;

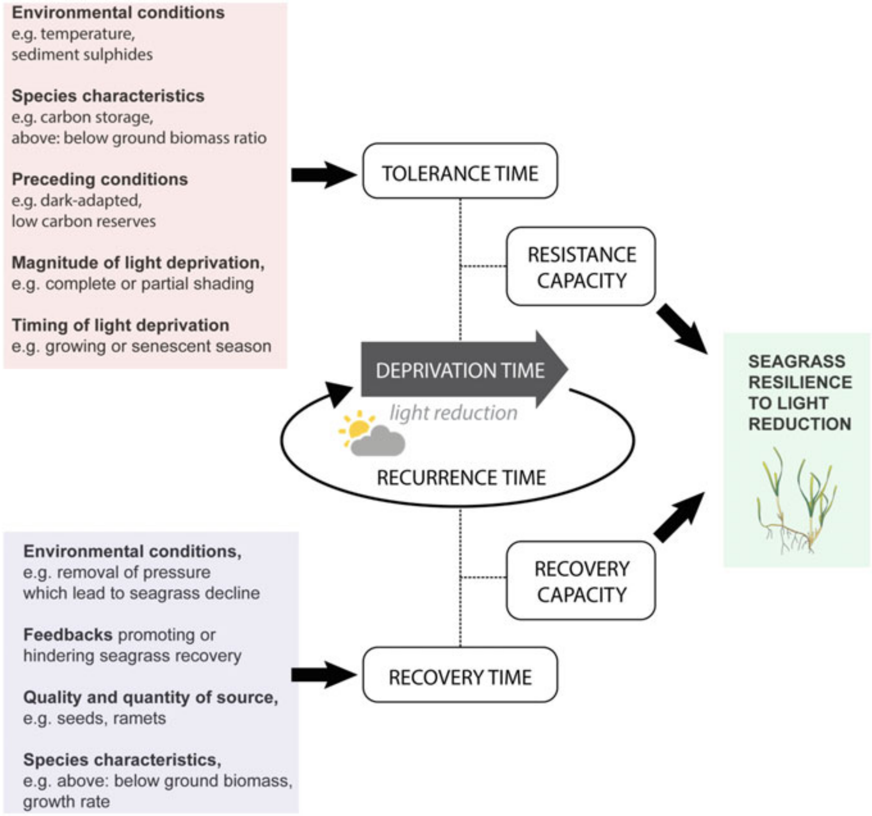


**Fig. 10.5** Conceptual figure of how species characteristics, duration and severity of the light decline, preceding light conditions and other environmental conditions affect the resilience of Australian seagrass ecosystems

Adams et al. 2017), or anoxic sediments (Hemminga 1998). For example, Collier et al. (2016) attributed higher tolerance times observed and predicted at 27.7 °C compared to 22.7 °C (Fig. 10.6) to higher respiration demands in warmer water. Environmental conditions which reduce photosynthetic efficiency, such as herbicide exposure (Negri et al. 2015), are also likely to reduce tolerance time. In contrast, increased availability of inorganic carbon increases photosynthetic efficiency (Ow et al. 2015), and hence may increase seagrass tolerance to light deprivation. Where growth and/or light availability are strongly seasonal, the timing of light deprivation can have a major impact on tolerance time, and hence resistance capacity (Burke et al. 1996; Alcoverro et al. 2001; Chartrand et al. 2016).

Preceding light conditions will also affect seagrass resistance to light decline, but this effect is difficult to predict. Phenotypic and genotypic plasticity means that seagrass populations that have adapted to poor light conditions may have higher resistance than populations of the same species adapted to better water quality

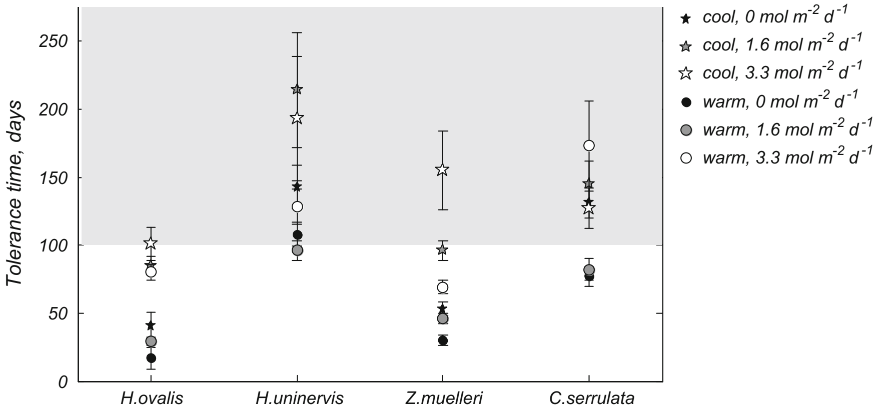


**Fig. 10.6** Tolerance time estimated from time taken for complete shoot loss for four tropical seagrass species, at three light levels and two temperatures (warm 27.7 °C, cool 22.7 °C), redrawn from (Collier et al. 2016). Experiments were conducted for 14 weeks. Tolerance times less than 14 weeks are observed (white area), tolerance times beyond 14 weeks are predicted from shoot density trajectories (shaded area). 95% confidence intervals are shown

conditions (Maxwell et al. 2014; Unsworth et al. 2015). Conversely, plants living quite close to minimum light requirements may have little capacity for further adaptation or carbon accumulation, making them vulnerable to loss even though biomass may be relatively high, e.g. Collier et al. (2009), Ferguson et al. (2016).

### *10.4.2 Resistance to and Recovery from Light Deprivation: Implications for Resilience*

Species-specific characteristics affect seagrass resistance to light deprivation, and subsequent recovery rates. Persistent seagrass species have the longest measured tolerance to light deprivation (Table 10.1, Fig. 10.7a). Typically these species have larger rhizomes and leaves (Fig. 10.7b, c), lower ratio of above to below ground biomass (Fig. 10.7d), and higher total biomass than other species (Fig. 10.7e).

While large, slow-growing persistent species exhibit the highest resistance to light deprivation, these large species are very slow to recover if leaves are shed to reduce self-shading (Erftemeijer et al. 2006). Carbon reserves may enable these plants to persist through acute light deprivation, but recovery is likely to be slow (Gordon et al. 1994; Collier et al. 2008). For example, *Posidonia* typically has a narrow window of recruitment opportunity, with small numbers of large seeds of relatively short longevity (Orth et al. 2006b; Kendrick et al. 2012; Ruiz-Montoya et al. 2012). Thus resistance underpins the resilience of persistent seagrass species to temporary light reduction, particularly where recovery is constrained by availability of source material, or inhibited by feedbacks (O'Brien et al. 2017).

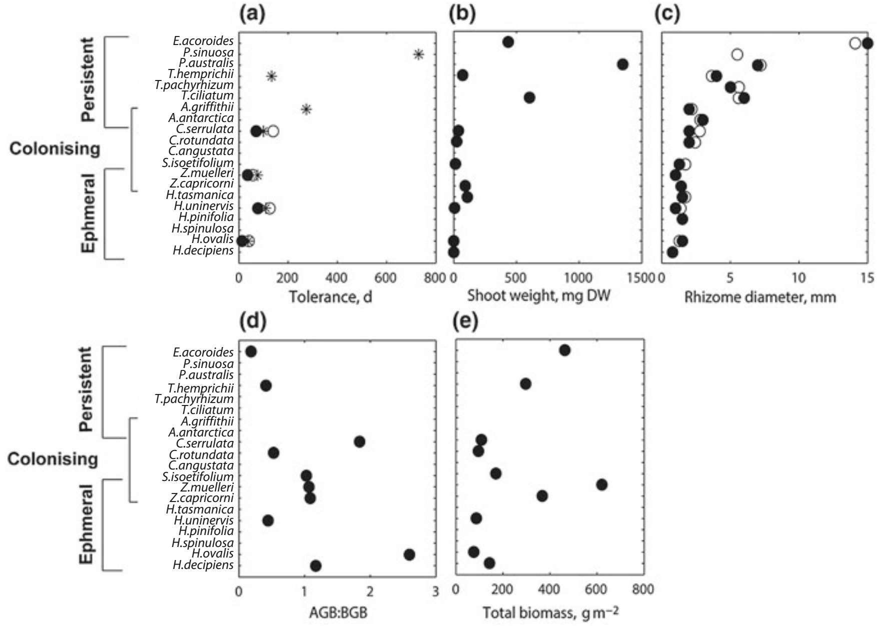


**Fig. 10.7** **a** Tolerance time in complete or near complete light deprivation (from Table 10.1: filled circles 27.7 °C, open circles 22.7 °C, *season not specified), **b** shoot weight (Duarte 1991a), **c** Rhizome diameter (filled circles Duarte 1991a, open circles Marba and Duarte 1998), **d** Ratio of above ground biomass (g DW $m^{-2}$) to below ground biomass (g DW $m^{-2}$) and **e** total biomass (Duarte and Chiscano 1999)

There appear to be trade-offs between seagrass characteristics which promote resistance to and recovery from light deprivation, and these are seen in the seagrass life history classification systems of Orth et al. (2006a) and Kilminster et al. (2015), previously discussed in Sect. 3.1. Whereas persistent genera such as *Posidonia* can resist extreme light deprivation for months or years (Fig. 10.7, Table 10.1), small colonising seagrasses are characterised by low resistance and rapid recovery. For example, biomass of *H. ovalis* can be completely lost in less than 6 weeks under 100% shading (Longstaff and Dennison 1999). Decline in carbon reserves of *H. ovalis* has been observed within 3 days of complete light reduction, and biomass within a week (Longstaff et al. 1999). While these plants have some carbon reserves, those reserves provide a limited buffer of approximately one month in complete absence of light, i.e. less than 5% of the tolerance time of much larger species. Thus the resilience of small, fast-growing seagrasses such as *Halophila* spp. arises from their large seed banks and high recovery rates, rather than resistance (Longstaff et al. 1999; Rasheed et al. 2014; Unsworth et al. 2015).

In contrast to persistent species, colonising seagrass may disappear rapidly during light reduction (e.g. Figure 10.6, 10.7a), but will be resilient if able to recover spontaneously when light availability improves. Colonising seagrass with short recovery times will be able to withstand a much higher frequency of light deprivation than large, slow-growing persistent species, which can take decades or centuries to recover from large-scale loss (Duarte 1995). The ability to recover from widespread loss will depend on the availability of seed stock and/or plant fragments (Kendrick et al. 2012; Rasheed et al. 2014), the scale of loss (van Katwijk et al. 2016), when light deprivation ends (Campbell and McKenzie 2004; van Katwijk et al. 2009) and the presence and strength of self-sustaining feedbacks inhibiting recolonization (Nyström et al. 2012; Maxwell et al. 2017). For example, loss and recovery are characteristic features of many seagrass communities in tropical Queensland, dominated by colonising and opportunistic species (Preen et al. 1995; Rasheed et al. 2014). However decline of large, persistent species in Cockburn Sound, WA (Kendrick et al. 2002) and Adelaide coastal waters, SA (Westphalen et al. 2004) have led to changes in environmental conditions which have inhibited recovery in the decades since seagrass decline.

Opportunistic seagrass species such as *Z. muelleri*, *H. uninervis*, *C. serrulata*, *T. hemprichii* and *A. griffithii* are able to use carbon reserves to survive light deprivation on the order of 2–9 months (Table 10.1). These opportunistic species have both: (a) higher recovery capacity than large persistent seagrasses; and (b) greater resistance capacity than small colonising species (Kilminster et al. 2015). The resilience of these species under light deprivation therefore depends on the intensity and timing of the event (Burke et al. 1996; Maxwell et al. 2014), and how well the subsequent environmental conditions promote recovery (Campbell and McKenzie 2004).

### *10.4.3 Recovery from Light Decline*

The establishment of a seed bank prior to the light reduction is critical to the resilience of colonising and opportunistic seagrasses (Rasheed et al. 2014). Transport of seeds from hydrodynamically connected source meadows can also enable recovery (Ruiz-Montoya et al. 2012; Unsworth et al. 2015). Without this seed bank or other source of propagules, recovery of the meadow cannot proceed by sexual reproduction.

Because the time since seed production is central to the viability of the seed bank (Jarvis et al. 2014), preceding conditions can affect seagrass recovery from, as well as resistance to, deterioration in light conditions. Environmental factors such as sediment depth and sediment type can also affect germination and survival of seedlings (Jarvis et al. 2014), while light or nutrient limitation can reduce flowering intensity (Jahnke et al. 2015).

Despite the important role played by recovery processes in ensuring the resilience of seagrass ecosystems, very little is known about the seed density required to initiate meadow recovery, and the impact of chronic stress and other acute stressors on flowering intensity and seed bank formation. This is a major gap for future research.

## 10.5 Conclusions

The capacity for resistance and recovery of Australian seagrass ecosystems will determine their resilience in the face of multiple light stressors associated with eutrophication, declining water quality, turbidity plumes and sea-level rise; as well as more stochastic perturbations such as cyclones which can amplify these persistent stressors. Both resistance and recovery depend on environmental conditions (which can affect both seagrass light requirements and recovery rates), species characteristics, diversity (within and between species), the timing and magnitude of the light deprivation, recovery capacity (e.g. seed bank size and condition) and the presence of feedbacks affecting recolonisation. Enhancing the capacity of seagrass ecosystems to resist and recover from light deprivation disturbance is therefore important for reversing global decline in this valuable habitat.

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# Part V

# Physiology

# Chapter 11
# Photosynthesis and Metabolism of Seagrasses

**Anthony W. D. Larkum, Mathieu Pernice, Martin Schliep, Peter Davey, Milan Szabo, John A. Raven, Mads Lichtenberg, Kasper Elgetti Brodersen and Peter J. Ralph**

**Abstract** Seagrasses have a unique leaf morphology where the major site for chloroplasts is in the epidermal cells, stomata are absent and aerenchyma is present inside the epidermis. This means that the major site for photosynthesis is in the epidermis. Furthermore the lack of stomata means that the route for carbon uptake is via inorganic carbon ($C_i$) uptake across the vestigial cuticle and through the outer plasma membranes. Since the leaf may at times be in an unstirred situation diffusion through an unstirred layer outside the leaf may be a large obstacle to carbon uptake. The existence of a carbon concentrating mechanism is discussed, but its existence to

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date is not proven. Active bicarbonate uptake across the plasmalemma does not seem to operate; an external carbonic anhydrase and an extrusion of protons seem to play a role in enhancing $CO_2$ uptake. There is some evidence that a C4 mechanism plays a role in carbon fixation but more evidence from "omics" is required. Photorespiration certainly occurs in seagrasses and an active xanthophyll cycle is present to cope with damaging high light, but both these biochemical mechanisms need further work. Finally, epiphytes pose a problem which impedes the uptake of $C_i$ and modifies the light environment inside the leaves.

## 11.1 Introduction

Seagrasses are representatives of at least three families of flowering plants that returned to the sea after the origin of embryophytes in a terrestrial environment at least 470 million years ago (Willis and McElwain 2014; see Chap. 1). Thus when this occurred, which best estimates put as long as 180–200 MA ago (see Chap. 1 Larkum and den Hartog 1989; Smith et al 2010; Olsen et al. 2016) most of the changes to the photosynthetic apparatus and pathways found today had taken place. The only major adaptations that occurred in tracheophyte photosynthesis were the evolution of C4 and CAM (Crassulacean Acid Matabolism) photosynthesis, that are forms of $CO_2$ concentrating mechanisms (CCM) (Raven and Beardall 2014, 2016). These CCMs allow terrestrial plants mainly in warmer climates to use less water in transpiration per unit $CO_2$ assimilated. CCMs also act similarly in emersed intertidal macroalgae, though the main role of CCMs in marine macroalgae is increasing the rate of photosynthesis per unit thallus area than occurs when there is diffusive movement of $CO_2$ with a very low diffusion coefficient from the bulk water to Rubisco (Surif and Raven 1990). CAM photosynthesis occurs in some submerged succulents, but not in seagrasses (Keeley 1998), and C4 photosynthesis apparently occurs in some seagrasses (see Sect. 11.3.4). Salinity in marine habitats was probably not a selection pressure for these changes in biochemistry since facultative expression of C4 photosynthesis is known from freshwater relatives of seagrasses in relation to limited inorganic C supply, and this could also apply to seagrasses. However, all the other major photosynthetic changes in seagrasses can clearly be seen as a response to the aqueous or saline environment; these changes were (i) loss of stomata, (ii) drastic reduction in the thickness of the cuticle, (iii) adaptations to a greater resistance pathway of $CO_2$ to the site of $CO_2$ fixation, (iv) the general but not obligate placement of chloroplasts in the epidermal cells of leaves (for the small occurrence of chloroplasts in mesophyll cells see: Barnabas 1982; Kuo 1984; Fernández et al. 1999; Larkum et al. 2017), and (v) shade adaptation of the light harvesting system and loss of PhyC phytochromes (Olsen et al. 2016). Of these, (i)–(iv) occur in close freshwater relatives of seagrasses, with no data available for the freshwater relatives on (v); phytochromes, of course, occur in many algae, and some still occur in seagrasses despite the loss of PhyC. Using cladistic terminology, traits (i)–(iv) are probably synapomorphies of the seagrasses and their close freshwater relatives rather than autapomorphies of seagrasses. In addition to these changes there are still unresolved questions concerning any effects of the salinity or osmolarity on the photosynthetic physiology of the seagrass leaves.

Much has been written on these aspects in recent years (see e.g. Larkum et al. 1989a, Chap. 20; Larkum et al. 2006, Chap. 14) and this chapter will concentrate on two aspects where recent work has led to recent clarification. These are (a) the uptake of inorganic carbon by the leaves of seagrasses, and (b) the biochemistry of carbon fixation in photosynthesis. And because the "omics" era promises new insights into the mechanism of carbon fixation in seagrasses special attention is paid to recent advances in this area. In addition, special attention is also given to the role of anatomical adaptions in seagrasses and the effect of epiphytes on their leaves.

## 11.2 Photosynthetic Adaptations of Seagrasses

### *11.2.1 Major Adaptations*

The major adaptions of seagrasses, which are found in all taxonomic groups, may be listed as:

(i) Loss of stomata. The loss of stomata can be understood in terms of their role as a control mechanism for the movement of $CO_2$ into and out of, and water vapour out of, vascular land plants. Additionally the partial loss of the ethylene pathway (Golicz et al. 2015) and the loss of other key volatiles (Olsen et al. 2016) can be related to loss of stomata. In seagrasses, as in submerged leaves of freshwater hydrophytes, stomata are not needed and have been dispensed with. Genes for stomata are lacking from the genome of *Z. marina* (Olsen et al. 2016). Gaseous hormones may not serve their role as well in an aqueous medium, as opposed to terrestrial plants existing in a gaseous medium (cf. Olsen et al. 2016). However, since gas spaces exist in seagrasses and would seem to serve as a useful medium for gaseous hormones, lack of time to evolve such internal mechanisms may be another factor.

(ii) Reduction of cuticle. The reduction of the cuticle to a relict layer of cutin means that the cuticle contains little or none of the waxy layer, which is the main component restricting the diffusion of ions such as $HCO_3^-$ and neutral molecules such as $CO_2$ and water (Fich et al. 2016). The minimal cuticle apparently reduces the resistance to diffusive $CO_2$ entry; however, as we shall see in the next subsection this does not fully solve the difficulty imposed by living in water and other adaptions are needed to overcome the high resistance of the pathway for $CO_2$ diffusion from bulk seawater into epidermal cells of seagrasses.

The existence of a relict cuticle suggests that this structure may still serve a function, although a convincing one has not been suggested to date. The cuticle could serve as a protective mechanism against pathogens or during the sloughing off of epiphytes (as in some macroalgae; see, e.g. Filion-Myklebust and Norton 1981). However, field observations of epiphytes show that the load can become severe on the older parts of leaves (see Sect. 11.4) and no difference in the three major lines of seagrass in terms of cuticle has been observed (J. Kuo, pers. comm.).

(iii) Adaptation to a diffusive boundary layer, in water, imposing a much larger relative restriction on diffusive $CO_2$ movement from the bulk phase to the epidermal surface thus creating a larger diffusive resistance than in land plants; a similar restriction applies in submerged freshwater macrophytes; the problem comes from the much lower (four orders of magnitude) diffusion coefficient for $CO_2$ in water compared to air.

(iv) The placement of the chloroplasts almost entirely in the epidermal cells, which reduces the length of the $C_i$ pathway to the site of $CO_2$ fixation, compared with submerged leaves of freshwater hydrophytes that maintain a strongly chlorophyllous sub-epidermal (mesophyll) leaf tissue (but see Sect. 11.3.1).

(v) Aerenchyma. The presence of aerenchyma is a general feature of a wide range of land plants (e.g. rice and sorghum) in response to flooding as well as their aquatic derivatives and even of submerged macroalgae (Sculthorpe, 1967), where it contributes also to buoyancy and gas exchange properties (Raven 1996). It is therefore not surprising that it is a feature of all seagrasses (Larkum et al. 1989a; Chap. 20).

(vi) Photosynthetic metabolism. The high transport costs of getting $C_i$ to the chloroplasts, even though they are all in the epidermal cells, has implications for downstream $CO_2$ fixation. The current whole genome investigations of seagrasses (Chap. 5) are beginning to reveal some of the possible mechanistic changes that have occurred and these are described in more detail in Sects. 11.3.4 and 11.3.5.

### *11.2.2 The Extra Costs of Living a Fully Submerged Life in Seawater*

Seagrasses generally live in full seawater (32–35‰) at a pH of ~8.0–8.2 and $HCO_3^-$ concentration of 2 mol $m^{-3}$. Under these conditions the concentration of $CO_2$ (ca 10 mmol $m^{-3}$ at 25 °C), which is about the same as that in air, is compounded by the much lower diffusivity in seawater. Thus while $CO_2$ is the substrate for Rubisco (the primary enzyme for inorganic carbon [$C_i$] fixation in photosynthesis), the most abundant source of $C_i$ is $HCO_3^-$, but this does not mean that it is automatically available; there are many marine and freshwater macroalgae, and freshwater macrophytes (most bryophytes, all pteridophytes, many flowering plants) that cannot use bicarbonate. As discussed in detail below (Sect. 11.2.3), the diffusive boundary layer (DBL) around seagrass leaves places severe restrictions on the diffusion of inorganic forms of carbon compared with aerial leaves, and has led to modifications of the epidermis and the cuticle.

As in the case of most hydrophytic plants, seagrasses are subjected to a higher light attenuation co-efficient than land plants, due to the different physical properties of air and water. As light penetrates the water column, it is progressively attenuated by absorption and scattering processes, which follow the Beer-Lambert Law. Seagrasses require significantly more incident light than most marine algae and freshwater angiosperms (mean of about 20% of the light at the sea surface light, with lowest values of about 5%, compared to 1% by some other angiosperms) (Dennison et al. 1993; Lee et al. 2007), and 0.00023% for the deepest-growing coralline red algae (Table 1 of Runcie et al. 2008). Furthermore, seagrasses often experience unfavorable environmental conditions whereby irradiance is reduced due to declining water quality (Ralph et al. 2007). On the other hand, inter-tidal dwelling seagrass meadows can be subjected to high irradiances of photosynthetically active radiation and UV radiation (Petrou et al. 2013). High rates of carbon fixation via photosynthesis are not possible under light limitation or high,

**Table 11.1** Photosynthetic rates (net photosynthesis, μmol $m^{-2}$ $s^{-1}$) at light saturation on total leaf area basis in near-present $CO_2$ concentrations in seawater, except for Borum et al. (2016) measured at near-saturating $CO_2$

| Species | Temperature | Rate | Reference |
|---|---|---|---|
| *Cymodocea nodosa* | | 2.9 | Drew (1978) |
| *Zostera marina* | 20 °C | 1.6 | Hellblom et al. (2001) |
| *Syringodium isoetifolium* | 26.5 °C | 3.35 | Pollard (1999) |
| *Halodule wrightii* | ? | 1.9[b] | Beer and Bjork (2000) |
| *Halophila ovalis* | ? | 1.5[b] | Beer and Bjork (2000) |
| *Posidonia australis* | ? | 0.3[a] | James and Larkum (1996) |
| *Zostera nolti* | 20 °C | 2.6 | Alexandre et al. (2012) |
| *Ruppia megacarpa* | 20 °C | 3.5[c] | Borum et al. (2016) |

Data presented in the references cited are assumed to be based on projected leaf area for planar leaves where this is not clear, so the values cited are half of the area-based rates in the references. Values in James and Larkum (1996) are on a total surface area basis; Alexandre et al. (2012) cited photosynthesis on a projected area basis (Alexandre, personal communication). Furthermore the cited photosynthetic values in Alexandre et al. (2012) were incorrect, and the values cited in Table 11.1 are correct

No Crassulacean Acid Metabolism in those seagrasses tested (Pärnik et al. 1992, who showed a slight 'reverse CAM' in *Thalassodendron ciliatum*, i.e. a lower cell sap pH and higher malic acid concenration in the photophase than in the scotophase; Keeley 1998 reviews other literature), and the values given in the Table are all for illuminated leaves

[a] Tris present, so DIC acquisition dependent on localized acidification of the leaf surface is inhibited

[b] Gross photosynthesis

[c] Value for near-saturating $CO_2$

photoinhibitory irradiances. Seagrasses however have the ability to acclimate to steep light gradients changing over variable periods of time. Since the ‘ *Biology of Seagrasses, Elsevier, 1989*’ (see Larkum et al. 1989a), many publications have added to our knowledge of such photosynthetic plasticity. Seagrasses maximise their photosynthetic performance, from the epigenetic level to the physiological level (Greco et al. 2013; Dattolo et al. 2013, 2014; Davey et al. 2016). The most widely known molecular and physiological changes we know of include: the regulation and conformational modification of Light Harvesting Complexes (LHCs) (Kong et al. 2016); regulation of chlorophyll levels and pigment ratios (Enríquez et al. 2002); regulation of accessory light capturing pigments (Silva et al. 2013); chloroplast clumping (Sharon 2010; Sharon et al. 2011); and the capacity to dissipate excess energy (Enríquez et al. 2002) including the regulation of the photo-protective xanthophyll cycle (Ralph et al. 2002; Petrou et al. 2013). It should be remembered that the transcriptional and translational control of light capture acclimation are much slower processes than the down-regulation of light energy by light harvesting antennae or through chloroplast clumping. To date the photo-physiology and biochemistry of light response and acclimation have been well studied in, but are not limited to, *Thalassia testudinum* (Durako, 1993; Enríquez et al. 2002), *Halophila stipulacea* (Sharon 2010), *Zostera marina* (Ralph et al. 2002; Silva et al. 2013), *Posidonia oceanica* (Figueroa et al. 2002), *Cymodocea nodosa* (Olivé et al. 2013; Silva et al. 2013) and several Australian species (Abal et al. 1994; Durako 2007; Horn et al. 2009; Petrou et al. 2013) (for a list of Australian species see Appendix).

### 11.2.3 The Photosynthetic Epidermis and Movement of $C_i$ to the Leaf Surface

Supply of $C_i$ to the seagrass leaf surface depends on the DIC concentration in the bulk medium outside the seagrass bed, and the extent of current and wave action and wind speed (Koch et al. 2006). Such movements increase the DIC flux to the interior of the seagrass bed and may decrease the leaf DBL thickness (Bryant et al. 2007), modulating the $CO_2$ flux between the atmosphere and the ocean surface (Ho et al. 2006; Semesi et al. 2009; Saderne et al. 2013). If there is a net positive $CO_2$ flux from the atmosphere into the meadow over a whole year then that meadow contributes to long-term storage of organic ‘blue carbon’ (see Chap. 22). At the same time, high concentrations of $O_2$ within the leaf due to low permeability of the leaf surface has several photosynthetic effects, such as increased production of reactive oxygen species (ROS) and increased photorespiration (see Black et al. 1976; Beer et al. 2002; Mass et al. 2010; Buapet et al. 2013).

### *11.2.4 Factors Affecting the Flux of Inorganic Carbon from the Bulk Water Phase to the Leaf Surface*

Control of the speed of laminar flow of water across macrophyte leaves along with measurements of the effective thickness of the DBL could be used to understand fluxes to the leaf surface in the natural environment; this has been done for a freshwater macroalga (MacFarlane and Raven 1985, 1989, 1990). However, few of these methods have been applied to seagrasses; James and Larkum (1996) assumed a minimal DBL thickness of 50 μm for their studies of *Posidonia australis* and following Briggs (1959) they calculated the uncatalysed $HCO_3^-$ to $CO_2$ conversion within the 50 μm DBL, and showed that the measured rate of photosynthesis could be accommodated if $CO_2$ was the only DIC source taken up by the seagrass, supplied by conversion from $HCO_3^-$. However, James and Larkum (1996) used Tricine (*N*-tris(hydroxymethyl)methylglycine) or CAPS (*N*-cyclohexyl-3-1minopropanesulfonic acid) buffers (depending on the pH); such buffers are now known to inhibit photosynthesis in many seagrasses (Hellblom et al. 2001; Koch et al. 2013). Table 11.1 shows that net photosynthesis by seagrasses in the absence of added buffers can be an order of magnitude greater at pH 8.0–8.2 than the values measured by James and Larkum (1996). Using a value of 3.3 μmol $m^{-2}$ leaf surface area $s^{-1}$ (Pollard 1999) the rate of uncatalysed $HCO_3^-$ to $CO_2$ conversions in a 50 μm thick DBL is only a fifth of what is needed, to supply $CO_2$ from $HCO_3^-$ at the leaf surface if $CO_2$ is the only form of $C_i$ entering the plant. In addition, the contribution of $CO_2$ diffusion across the DB layer must be considered, as outlined below.

For comparison, we calculated the possibility of a diffusive $CO_2$ flux from the bulk water phase to the leaf surface, with $CO_2$ entry into the leaf, for bulk phase $CO_2$ in equilibrium with a 400 μmol $mol^{-1}$ $CO_2$ gas phase; from Table 4.1 of Raven (1984) this concentration in seawater at 25 °C and 35‰ salinity yields the relatively low concentration of 11.6 mmol $m^{-3}$. With a $CO_2$ diffusion coefficient of $1.9 \times 10^{-9}$ $m^2$ $s^{-1}$ (Table 4.1; Raven 1984) and a $5 \times 10^{-5}$ m thick DBL, the permeability of the DBL is $1.9 \times 10^{-9}$ $m^2$ $s^{-1}/5 \times 10^{-5}$ m or $3.8 \times 10^{-5}$ m $s^{-1}$. Using the photosynthetic rate of $3.3 \times 10^{-6}$ mol $m^{-2}$ $s^{-1}$ (Pollard 1999), the concentration difference for $CO_2$ across the DBL is computed as 87 mmol $m^{-3}$, i.e. more than the external concentration of 11.6 mmol $m^{-3}$. Thus, even the uncatalysed production of $CO_2$ from $HCO_3^-$, considered in the preceding paragraph together with diffusion of $CO_2$ across the DBL cannot supply sufficient $CO_2$ for photosynthesis if $CO_2$ is the only $C_i$ form that enters the plant. However, as detailed below seagrasses have evolved ways that meet the photosynthetic demand adequately in their given environments in terms, as outlined below, of enhanced carbonic anhydrase activity on the outer side of seagrass leaves, and surface acidification.

A further potential restriction on $CO_2$ diffusion from the bulk water phase to the plasmalemma is the cuticle. There seem to be no measurements of the $CO_2$ permeability of seagrass cuticle, but there are values for the isolated cuticle of the submerged freshwater flowering plant *Vallisneria spiralis* (MacFarlane 1992), a close relative to the seagrasses *Enhalus*, *Halophila* and *Thalassia*. The isolated cuticle has a permeability to $CO_2$ of 2.1 μm $s^{-1}$ (and 3.3 μm $s^{-1}$ for $O_2$); removal of waxes increased the permeability to 7.7 μm $s^{-1}$ for $CO_2$ (and 9.6 μm $s^{-1}$ for $O_2$) (MacFarlane 1992). For a $CO_2$ influx in photosynthesis of 3.3 μmol $m^{-2}$ $s^{-1}$ the concentration difference across the cuticle is 1.1 μmol $m^{-3}$. This is less than 1% of the constraint imposed by the DBL. Other work on the permeability of the cuticle of freshwater submerged flowering plants (*Potamogeton* spp.) have only used $O_2$, with values of 6–33 μm $s^{-1}$ for cuticles 35–49 nm thick (Frost-Christensen et al. 2003). The cell wall permeability is at least three times that of the cuticle (Frost-Christensen et al. 2003).

Photosynthesis clearly does occur in seagrasses despite the result of the calculation of the need for a rate faster than permitted by the combination of uncatalysed production of $CO_2$ from $HCO_3^-$ and diffusion of $CO_2$ across the DBL. These high rates of photosynthesis can come about (i) from $HCO_3^-$ flux across the DBL, followed by direct $HCO_3^-$ influx as part of a CCM, (ii) by catalysed $HCO_3^-$ conversion to $CO_2$ using a cell wall carbonic anhydrase followed by diffusive $CO_2$ entry, or (iii) by external carbonic anhydrase plus localized surface acidification as part of a CCM. These processes are considered in 11.2.5 below. The processes all increase the potential for photosynthesis by permitting a major role of $HCO_3^-$ diffusion across the DBL. The $HCO_3^-$ concentration in the bulk seawater is at least 100 times that of $CO_2$ and the diffusion coefficient for $HCO_3^-$ is about half of that for $CO_2$, permitting $HCO_3^-$ fluxes to the cell surface of up to 50-fold that for $CO_2$ (Raven 1984). These high fluxes are permitted if acid-base and charge balance are maintained by parallel buffered fluxes of $H^+$ from the bulk phase to the epidermal cell wall and/or a buffered $OH^-$ flux in the opposite direction (Raven and Hurd 2012).

While the DBL effects on seagrass photosynthesis is generally attributed to the influence on $C_i$ supply, there is evidence (Mass et al. 2010) that restrictions on the $O_2$ efflux from the leaf also has a significant role in *Halophila stipulacea*. Such restrictions, the reverse of those for $O_2$ as far as the diffusive fluxes are concerned, increase the steady-state concentration of $O_2$ inside the photosynthesing leaf and hence allow for increased levels of ROS, as well as enhancing the activity of Rubisco oxygenase activity relative to Rubisco carboxylase, and hence the production of phosphoglycollate and photorespiration (see Sect. 11.3.5).

### *11.2.5 Movement of Inorganic Carbon Through the Plasmalemma*

Current evidence implies that $HCO_3^-$ influx (i.e. active $HCO_3^-$ uptake) does not occur in seagrass leaves based on evidence of a putative anion transporter or the action of the bicarbonate transport inhibitors, DIDS (4,4′-di-isothiocyanostilbene-2,2′-disulfonic acid) and SITS (4-acetamido-4′-isothiocyanostilbene-2,2′-disulfonic acid) (Larkum et al. 2006; Koch et al. 2013). An alternative suggestion for “active” $HCO_3^-$ entry is coupling it to known active $H^+$ extrusion pumps (Pak et al. 1995;

Fernández et al. 1999; Muramatsu et al. 2002; Kong et al. 2014), presumably via $H^+$–$HCO_3^-$ symport; this speculation also has little support (Larkum et al. 2006). There seems to have been no follow-up to the work of Millhouse and Strother (1986) on salt-dependent $HCO_3^-$ use in *Zostera muelleri*, although $Na^+$ cotransport of $NO_3^-$ and $H_2PO_4^-/HPO_4^{2-}$ has been shown for *Zostera marina*, which could be energized by active electrogenic $H^+$ efflux and a $Na^+$–$H^+$ antiport (Fernández et al. 1999; García-Sánchez et al. 2000; Brett et al. 2005; Rubio et al. 2005; Garciadeblás et al. 2007; Rubio et al. 2011; Olsen et al. 2016).

With little evidence to support the idea of $HCO_3^-$ transport across the plasmalemma, studies of the $C_i$ used by seagrasses have focused on the extracellular conversion of $HCO_3^-$ to $CO_2$, with uptake of $CO_2$ and its utilisation in photosynthesis. One possibility that has significant support is extracellular carbonic anhydrase (CA) activity, based on the inhibition of photosynthesis by the membrane-impermeant CA inhibitor acetazolamide (AZ: see Beer and Rehnberg 1997; James and Larkum, 1996; Larkum et al. 2006; Koch et al. 2013; Borum et al. 2016; Larkum et al. 2017). The relatively low sensitivity of the CA assay means that the lack of detectable activity (Millhouse and Strother 1986; Mercado et al. 2003; Demir et al. 2006) does not necessarily mean there is insufficient activity to be significant in $HCO_3^-$ acquisition, as indicated by acetazolamide (AZ) inhibition (Millhouse and Strother 1986). However, the use of AZ as an external CA specific inhibitor depends on its membrane impermeability and its specificity for CA, in seagrasses. Recently, a membrane bound external carbonic anhydrase (CAe) has been predicted in three Caribbean coral species based on kinetic studies of $^{18}O$ exchange (Tansik et al. 2015). This would be a feasible method for seagrasses too. Furthermore, CA genes have been found to be present in the genome of *Zostera marina* (Olsen et al. 2016), and regulated at the transcript level in *Zostera muelleri* in response to low $O_2$ conditions (Kim et al. submitted). However, the locations in which these genes are expressed in the plant is not yet known.

Another possibility, in addition to external CA, for enhancement of $CO_2$ entry is the involvement of the active $H^+$ efflux pump mentioned above (Larkum et al. 2006). Fernández et al. (1999) examined the green mesophyll cells of *Zostera marina* leaves, showing the presence of an electrogenic $H^+$ efflux pump energized by ATP provided by mitochondrial respiration (Carr and Axelsson 2008), as is the case for other tracheophytes, the ancestral charophycean green algae and the transcriptome of *Z. marina* (Kong et al. 2014). As suggested by Walker et al. (1980) in the context of ecorticate freshwater characeans with their alternating acid (based on active $H^+$ efflux) and alkaline zones along the internodal cells, the acid zones have two effects on the $HCO_3^-$ to $CO_2$ conversion: one is the effect on the equilibrium ratio of $CO_2$ to $HCO_3^-$, with an order of magnitude increase in the ratio for each unit pH decrease; the other effect is the enhancement of the (otherwise) uncatalysed $HCO_3^-$ conversion to $CO_2$ rate, again by an order of magnitude for each unit pH decrease. Even these enhancements may not be adequate to supply $CO_2$ at a rate sufficient to account for the observed rate of DIC assimilation in photosynthesis and, as indicated above, most seagrasses have a requirement for extracellular CA activity for adequate photosynthesis as indicated by AZ inhibition

(Larkum et al. 2006; Koch et al. 2013; Borum et al. 2016). At present there is no direct evidence for the acid zones in seagrass, any such zones are clearly smaller than those in the *Characeae* or certain freshwater submerged macrophytes otherwise they would be readily detected by pH indicators in unstirred media (Raven and Hurd 2012). The occurrence of such localized acid zones is despite the overall increase in pH at the surface of cells and tissues/organs photosynthesizing under water with pH and charge balance maintained, as indicated in 11.2.4 above, by buffered fluxes of $H^+$ from the bulk phase to the epidermal cell wall and/or a buffered $OH^-$ flux in the opposite direction (Raven and Hurd 2012).

The occurrence of the acid zone mechanism is indicated by the use of pH buffers such as Tris, as shown for an ecorticate freshwater characean (Price and Badger 1985) and, in the case of seagrasses, initially used to limit pH changes resulting from photosynthesis and respiration (see Hellblom et al. 2001; Beer et al. 2002; Hellblom and Axelsson 2003). Inhibition of photosynthesis by buffers is consistent with the use of the acidification mechanism in many seagrasses (Hellblom et al. 2001; Beer et al. 2002; Hellblom and Axelsson 2003; Koch et al. 2013; Uku et al. 2005; Burnell et al. 2014; Borum et al. 2016). Hellblom and Axelsson (2003) discuss the complex interactions of buffers such as the commonly used Tris buffer with the DIC system, concluding that Tris is still appropriate to indicate the occurrence of acid zones if they existed on the surface of seagrasses.

Given an enhancement of $CO_2$ concentration at the outer epidermal surface, $CO_2$ influx in photosynthetic cells of seagrasses as $CO_2$ could be delivered solely by diffusion through the lipid component of the plasmalemma, or involve supplementation of $CO_2$-selective proteinaceous channels such as $CO_2$-selective aquaporins (Raven and Beardall 2016): where there is still controversy over the $CO_2$ permeability coefficient for the lipid phase of the plasmalemma, and hence of the role of the $CO_2$-selective aquaporins characterised from the plasmalemma of some terrestrial $C_3$ flowering plants. On the basis of the area of mesophyll cells exposed to intercellular gas spaces in $C_3$ terrestrial plants the rate of photosynthesis, at a photosynthetic photon flux density at a projected leaf area basis of $1000\ \mu mol\ m^{-2}\ s^{-1}$, is $1\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$ at the present atmospheric $CO_2$ concentration in the intercellular gas spaces (Fig. 8–16 of Nobel 2005). This $1\ \mu mol\ m^{-2}\ s^{-1}$ is only about a third of the highest rate of photosynthesis on a total leaf surface area basis of seagrasses (Table 11.1), making the case for mediated $CO_2$ influx stronger.

An important possibility is that one or more of the mechanisms that rely on transport of $HCO_3^-$ (other than extracellular CA without localized acidification) can act as a $CO_2$ concentrating mechanism (CCM) (Schwarz et al. 2000; Beer et al. 2002). The combination of acid zones and external CA could yield a $CO_2$ concentration at the leaf surface that was several times that in the bulk seawater; and with a sufficiently high permeability of the plasmalemma to $CO_2$ (see above) a high enough $CO_2$ concentration could also occur in the cytosol. Recently, a mechanism incorporating both an $HCO_3^-$/proton cotransporter together with a proton extrusion pump as in Fig 11.3 has been proposed in *Posidonia oceanica* (Rubio et al. 2017). This model can also incorporate an external carbonic anhydrase. However a large part of the evidence on which this was based was the use of microelectrodes placed in the cytoplasm of mesophyll cells, which may show different membrane and metabolic properties to the outer epidermal cells where much of the photosynthesis occurs.

## 11.3 Biochemical Aspects of Photosynthetic Carbon Fixation

### *11.3.1 Movement of Inorganic Carbon from the Plasmalemma to the Site of Carboxylation*

The intracellular $C_i$ pathway from the outer face of the plasmalemma to the carboxylation site (Fig. 11.1) imposes a restriction on the rate of photosynthesis termed (for C3 terrestrial tracheophytes) the 'mesophyll resistance'. The reciprocal, 'mesophyll permeability' is defined as the quotient of the rate of photosynthesis on an area basis (mol $CO_2$ $m^{-2}$ $s^{-1}$) and the difference in concentration of $CO_2$ between the outer surface of the plasmalemma and the carboxylation site (mol $CO_2$ $m^{-3}$), i.e. including the plasmalemma permeability (see also Fig. 11.3, Larkum et al. 1989b). The units of the mesophyll $CO_2$ permeability are m $s^{-1}$, i.e. the same units as for the permeability of the DBL. For $C_3$ terrestrial embryophytes, the mesophyll permeability is, expressed as the averages for a range of flowering plants, and $C_3$ terrestrial bryophytes, $0.80 \times 10^{-4}$ to $2.24 \times 10^{-4}$ m $s^{-1}$ (Table 2 of Raven and Beardall 2016). As a result of the unique anatomy of seagrasses with chloroplasts almost entirely restricted to the leaf epidermis, and lack of stomata and a lack internal air spaces in the mesophyll, there is in fact a greater distance from the plasmalemma to the site of Rubisco compared to most terrestrial $C_3$ embryophytes (Kuo and den Hartog 2006) and thus the equivalent of mesophyll permeability in seagrasses is probably lower than in the land embryophytes, i.e. this imposes a greater restriction on the rate of photosynthesis in seagrasses than in the terrestrial plants. Thus the rate of photosynthesis in seagrasses is likely to be lower than for equivalent conditions in land embryophytes. However, the rate of photosynthesis on the basis of the area over which inorganic carbon crosses the fluid medium/cell wall interface is higher than in land plants.

Specialised "transfer cells" have been observed in a variety but not all seagrasses (Larkum et al. 2017). These transfer cell occur on the inner tangential walls of epidermal cells. They may have a function in the transport of $C_i$ but at this stage this remains speculative (Larkum et al. 2017).

### *11.3.2 C3 Versus C4 Metabolism*

For seagrasses with a putative $C_4$ metabolism (see Sect. 11.3.4), or with non-biochemical CCMs, the photosynthetic rate is decreased if a higher fraction of CCM pumped into the cells leaks out; very little is known about this for seagrasses (see Raven and Beardall 2016).

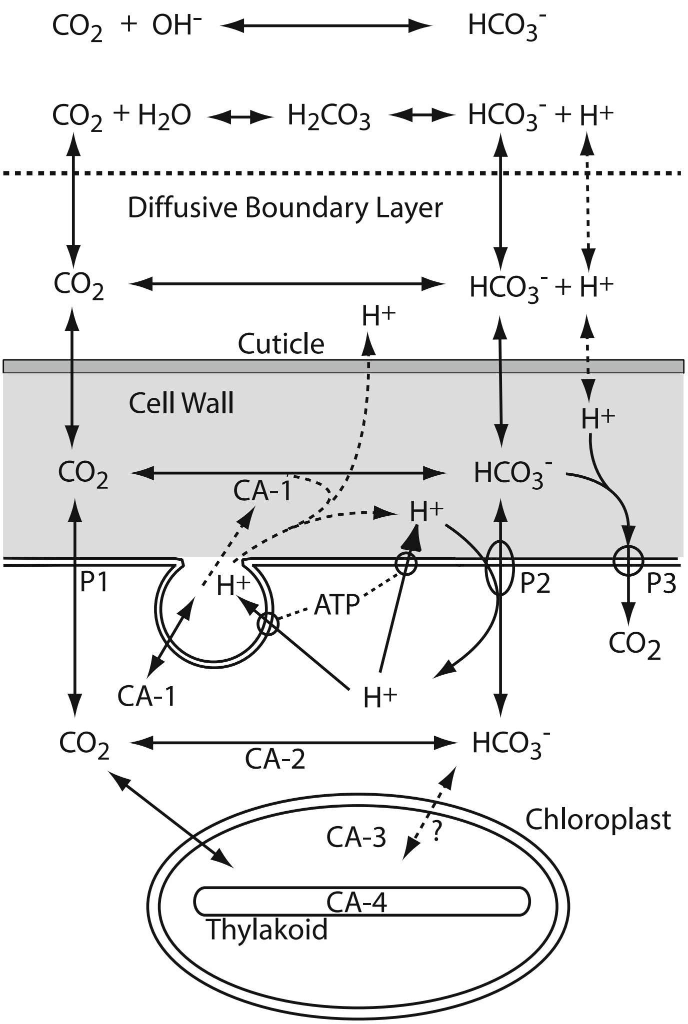


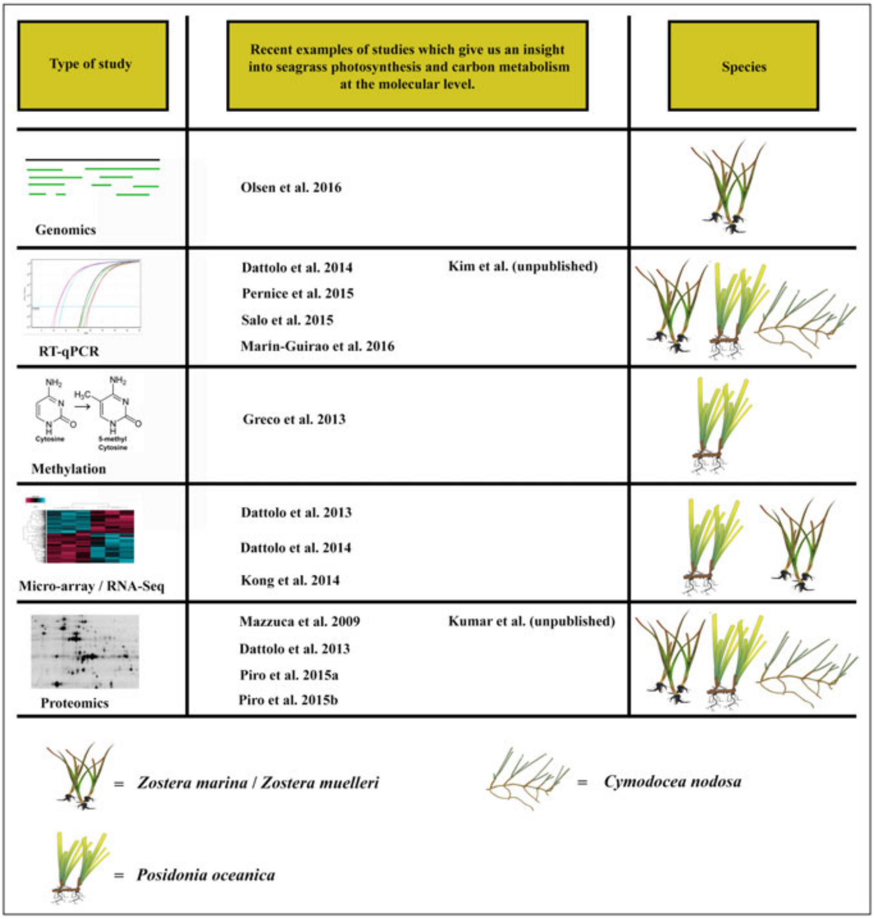
**Fig. 11.1** Diagram of possible transport mechanisms for $CO_2/HCO_3^-$ at the outer surface of the epidermal cell of seagrasses (adapted from Larkum et al. 2006). CA-1, i.e. carbonic anhydrase excreted from epidermal cells; CA-2, cytoplasmic carbonic anhydrase; CA-3, carbonic anhydrase of the chloroplast stroma; CA-4, carbonic anhydrase of the thylakoid inner space. Note that while the diagram apparently shows a coupled bicarbonate and proton movement across the plasmalemma this is not implied as there are no known proton-driven bicarbonate pumps. Any active movement of bicarbonate would have to be driven by chloride, sodium, etc. and such coupled systems are known

The physiology of seagrasses generally resembles that of $C_3$ terrestrial plants, with a continuously downhill diffusive flux of $CO_2$ from the bulk phase to Rubisco, although, as shown in 11.2.4 and 11.2.5 above, the $CO_2$ flux in seagrasses is augmented by $HCO_3^-$, and buffered $H^+/OH^-$, fluxes in parallel with $CO_2$ and intra- and extra-cellular carbonic anhydrases. The general lack of saturation of photosynthesis in air-equilibrium seawater (Beer and Rehnberg 1997; Beer et al. 2002; Zimmerman et al. 1997; Larkum et al. 2006; Koch et al. 2013; Borum et al. 2016) is qualitatively consistent with diffusive $CO_2$ entry; an exception is *Cymodocea serrulata* where $CO_2$ saturation in air-equilibrated seawater is consistent with a CCM (Schwarz et al. 2000). Diffusive $CO_2$ entry is also qualitatively consistent with the $O_2$ inhibition of photosynthesis in air-equilibrium seawater relative to very low $O_2$ and air-equilibrium $CO_2$ concentrations (Black et al. 1976 [10 min data only]; Downton et al. 1976; Beer et al. 2002; Buapet et al. 2013). In some cases the $CO_2$ compensation concentration, from the pH compensation value of 9 or below, is consistent with diffusive $CO_2$ entry, although in other cases the pH compensation concentration is above pH 9, a value consistent with the occurrence of a CCM (Beer et al. 2006; Jiang et al. 2010; Borum et al. 2016). However, the occurrence of significant labelling of photorespiratory carbon oxidation cycle intermediates shows incomplete suppression of Rubisco oxygenase activity (Andrews and Abel 1979). The natural abundance ratio of $^{13}C$ to $^{12}C$ in seagrass organic matter (Raven et al. 2002; McPherson et al. 2015; Stepien 2015) has been of little help in determining the mechanism of DIC entry or distinguishing $C_4$ from $C_3$ photosynthetic biochemistry.

To expand on $\delta^{13}C$ in seagrasses, the values are from about −5‰ to slightly more positive than −20‰. Although $\delta^{13}C$ values are always higher than −30‰, this does not necessarily rule out diffusive entry of $CO_2$ to Rubisco in view of the large values for the DBL resistance and/or the internal diffusion restriction (i.e. the "mesophyll resistance" of $C_3$ terrestrial plants) that can cause a "$CO_2$ diffusion" macrophyte to have a $\delta^{13}C$ higher than −30‰. Seagrass $\delta^{13}C$ values in the range −10 to −20‰ do not distinguish entry of $CO_2$ from that of $HCO_3^-$. There are considerable problems with using $\delta^{13}C$ to distinguish $CO_2$ influx (in a CCM or by a component of diffusion from the bulk medium to Rubisco) from $HCO_3^-$ influx into a cell of a seagrass with a CCM. Furthermore, this range of $\delta^{13}C$ values does not distinguish direct $HCO_3^-$ entry from $HCO_3^-$ conversion to $CO_2$ in an acidic micro-environment where CA catalysis might show kinetic isotope discrimination rather than equilibrium isotope discrimination. Finally for $C_i$ entry into seagrasses with $\delta^{13}C$ values between −10 and −20‰, $C_4$ biochemistry with carboxylation using phosphoenolpyruvate carboxyase (PEPC) has $\delta^{13}C$ values between −10 and −20‰, but $\delta^{13}C$ cannot distinguish $C_4$ from other (biophysical) CCMs in seagrasses. $\delta^{13}C$ has been used as a (rather unreliable) estimate of $CO_2$ leakage from CCMs in microalgae with $\delta^{13}C$ values between −10 and −30‰; this assumes that the $\delta^{13}C$ of the inorganic C form entering is known, and the estimates of $CO_2$ leakage in the text of Raven and Beardall (2016) only use values from membrane inlet mass spectrometry (MIMS) either during photosynthesis when $HCO_3^-$ is known to be the sole inorganic carbon species entering or, when this is not the case, MIMS estimates of $CO_2$ efflux just after cessation of illumination are used. This has not been performed with seagrasses. However, a definite conclusion can be drawn from $\delta^{13}C$ values more positive than −10‰: such values can only be explained by $HCO_3^-$ influx or by an extracellular carbonic anhydrase plus a localized acid zone mechanism (11.2.4 above).

### *11.3.3 Insight into Seagrass Photosynthesis Through Next Generation Sequencing*

In the recent past, next-generation sequencing technology has been applied to seagrass research to improve our understanding of seagrass photosynthesis and carbon metabolism (Mazzuca et al. 2013; Pernice et al. 2015; Davey et al. 2016; and see Fig. 11.2), which has led to an increased knowledge of both photosynthetic plasticity and diversity at the genetic level (see Fig. 11.3). The recently published genome of *Z. marina* (Olsen et al. 2016) has provided novel insights into the differences between selected plants and seagrasses. *Z. marina* has lost the *UVR8*



| Type of study | Recent examples of studies which give us an insight into seagrass photosynthesis and carbon metabolism at the molecular level. | Species |
|---|---|---|
| Genomics | Olsen et al. 2016 | |
| RT-qPCR | Dattolo et al. 2014<br>Pernice et al. 2015<br>Salo et al. 2015<br>Marin-Guirao et al. 2016<br>Kim et al. (unpublished) | |
| Methylation | Greco et al. 2013 | |
| Micro-array / RNA-Seq | Dattolo et al. 2013<br>Dattolo et al. 2014<br>Kong et al. 2014 | |
| Proteomics | Mazzuca et al. 2009<br>Dattolo et al. 2013<br>Piro et al. 2015a<br>Piro et al. 2015b<br>Kumar et al. (unpublished) | |

= *Zostera marina* / *Zostera muelleri*

= *Cymodocea nodosa*

= *Posidonia oceanica*

**Fig. 11.2** Omics-based studies since the year 2009. These literature citations are examples of studies which have provided us with novel information on carbon metabolism and photosynthesis at the molecular level within a range of seagrass species

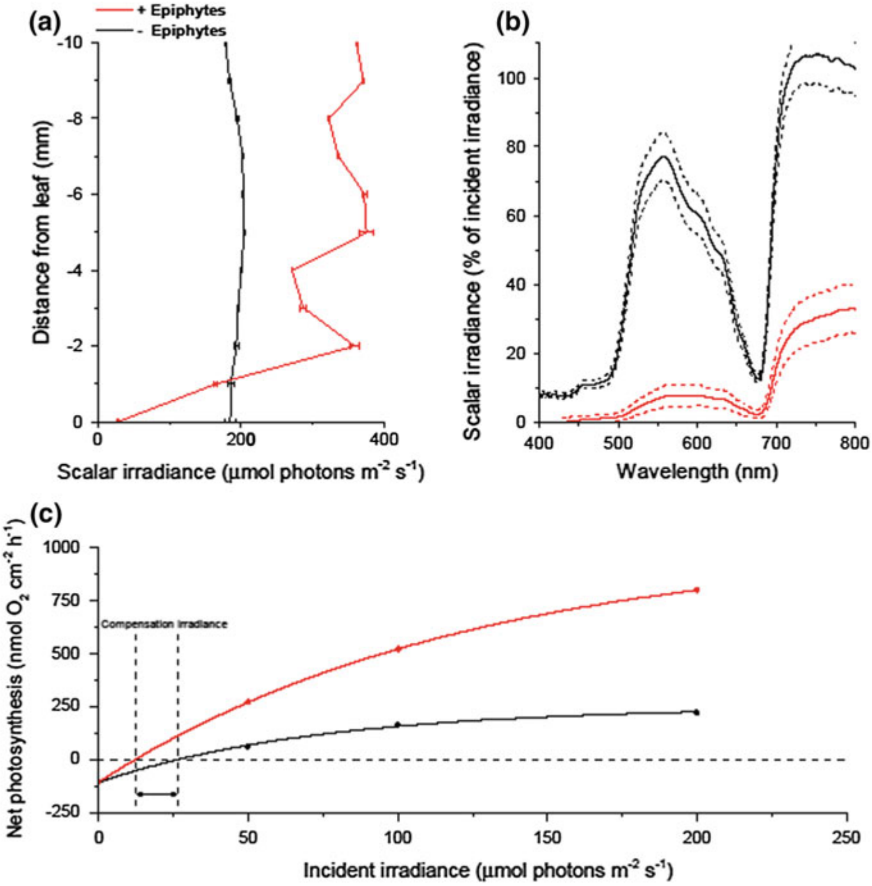


**Fig. 11.3** **a** Light microclimate around seagrass leaves of *Z. marina* with- and without epiphyte cover. Profiles are measured as scalar irradiance of PAR light (400–700 nm) at an incident irradiance of 200 µmol photons $m^{-2}$ $s^{-1}$. **b** Transmission light spectra of leaves with- and without epiphyte cover (incident irradiance of 200 µmol photons $m^{-2}$ $s^{-1}$). **c** Photosynthesis-irradiance curves of net photosynthesis measured from the flux of $O_2$ across the diffusive boundary layer, in leaves with- and without epiphyte cover. Figure redrawn with permission from Brodersen et al (2015b)

gene involved in UV detection, and *PHYC* gene involved in far red light response and flowering. An expansion of the Light Harvesting Complex B (LHCB) superfamily is suggested (Olsen et al. 2016). Such modifications in the genome are logical given that seagrasses live a submerged lifestyle. Nevertheless blue light receptors would be expected to play an important role in seagrasses as in many algae; and it should be noted that a cryptochrome and phototropin genes were also found in *Z. marina* (Kong et al. 2014; Olsen et al. 2016).

### *11.3.4 Seagrass Photosynthetic Systems Are Still Elusive*

The recent review by Davey et al. (2016) suggests various possible modes of photosynthesis throughout this small but unique group of angiosperms. On inspection, the features of seagrasses are more closely associated with C4 plant features than C3 plants, hence the confusion surrounding occurrence of these two processes; for example, the occurrence of a Carbon Concentrating Mechanism (CCM) in at least some seagrasses has been suggested (Borum et al. 2016; Larkum et al. 2017) The first instance of associating seagrasses with C4-like behavior was by Benedict and Scott (1976) when they suggested that the tropical seagrass, *Thalassia testudinum* was a C4 plant. In that study values were obtained for $\delta^{13}C$ analysis that were more like those for terrestrial C4 rather than for terrestrial C3 plants, although, as discussed above, $\delta^{13}C$ measurements on seagrasses are difficult to interpret. Additionally, mesophyll cells in *T. testudinum* were found to exist which contained chloroplasts with under-developed lamellae, suggesting C4 like arrangement; however, on closer inspection Benedict et al. (1980) later withdrew this hypothesis, suggesting the values observed were due to what would now be termed low leakage of $CO_2$ from a CCM. The interpretation of $\delta^{13}C$ values in aquatic plants is very complex, due to the presence of the diffusive boundary layer, which surrounds the leaves as well as $HCO_3^-$ use and the possible occurrence of CCMs and maybe including a $C_4$ mechanism (see Sect. 11.2).

For a long time, ‘Kranz anatomy’ was regarded as an obligatory requirement to classify a plant as a C4 autotroph. Whilst there is no knowledge indicating that seagrasses contain photosynthetically competent bundle sheath cells (Kuo and den Hartog 2006), and while almost all species have their chloroplasts largely restricted to the epidermis, investigations into the freshwater hydrophyte *Hydrilla verticillata* (*Hydrocharitaceae*; Bowes et al. 2002; Bowes 2011; Davey et al. 2016) have established that single cell C4 type photosynthesis occurs independent of true Kranz anatomy. Enzymatic activity and gene expression of phosphoenylpyruvate carboxylase (PEPC) and CA have been detected in seagrasses (Muramatsu et al. 2002; Olsen et al. 2016; Kim et al. unpublished; Kumar et al. unpublished). PEPC, however, is involved in supplying oxaloacetate to the citric acid to replace intermediates (oxaloacetate, 2-oxoglutarate) that are removed in the synthesis of some amino acids, pryimidines, haems and chlorins, as well as in intracellular acid-base regulation (Raven 1984; Aubry et al. 2011; Doubnerová and Ryšlavá 2011; Chi et al. 2014). The other enzymes involved in $C_4$ photosynthesis are also involved in reactions other than $C_4$ photosynthesis (Raven 1984; Wheeler et al. 2005; Aubry et al. 2011; Doubnerová and Ryšlavá 2011; Chi et al. 2014). Caution should therefore be exercised until evidence provides a better basis for such an hypothesis.

The least ambiguous method of determining the occurrence of C3, C3-C4 intermediate, or C4 metabolism is the short-term (seconds to tens of seconds) kinetics of labelling of organic compounds from external $^{14}C$-inorganic C (Andrews and Abel 1979; Beer et al. 1980). Most of the data are consistent with $C_3$ biochemistry, but *Halophila stipulacea* has labelling consistent with a C3-C4 intermediate pathway *and Thalassia hemprichii* has labelling consistent with C4 biochemistry (Andrews and Abel 1979; Beer et al. 1980; see also Waghmode and Joshi 1983; Reiskind et al. 1997); however, these data remain essentially untested. Kim's recent work (unpublished) on *Z. muelleri* has suggested this Australasian species possesses C3-like behaviour in response to low $O_2$ levels, uncharacteristic of C4 behaviour. With NGS technology coming to the forefront (Davey et al. 2016); nanoSIMS and 14-C labelling can perhaps be used in combination with this technology to provide a long awaited test of such an hypothesis.

### *11.3.5 Photorespiration*

Rubisco, the most abundant enzyme in the world, is primarily known for its key role in the carboxylation of ribulose bisphosphate (RuBP) in the initial step of the Calvin Benson cycle to produce 2 molecules of 3-Phosphoglycerate. In contrast, low $CO_2$ and high $O_2$ environments increases the oxygenase activity of Rubisco relative to the carboxylation activity, due rather to changes in substrate concentrations than affinity changes. Rubisco oxygenase has initial products of 1 molecule of phosphoglycerate and 1 molecule of phosphoglycolate (which is quickly converted to glycollate) for each molecule of RuBP. Then, in the process of photorespiration, peroxisomes convert glycolate to triose phosphate. Photorespiration not only decreases gross photosynthetic carbon fixation, but also utilizes ATP and reducing agents, which could otherwise be used in carbon fixation, and, more over, produces $CO_2$. However, the energy cost of photorespiration can often be less than that of its suppression using a $CO_2$ concentrating mechanism, especially at low temperatures (Raven and Beardall 2014; Raven et al. 2014). In terrestrial tracheophytes, phosphoglycolate, the product of Rubisco oxygenase is toxic when accumulated, but it is dephosphorylated to glycolate within the chloroplast, and then in turn it is transported to the peroxisomes where it is oxidized by glycolate oxidase to glyoxylate and aminated or transaminated forming glycine. The glycine is then decarboxylated in mitochondria to form 1 serine from 2 glycine, recycled through the peroxisome and chloroplast where it is converted into hydroxypyruvate, glycerate and 3-phophoglycerate and then triose phosphate, which can be recycled in the Calvin Benson cycle to regenerate RuBP. Whilst this is the generalized photorespiratory carbon oxidation cycle, further work in seagrasses needs to be conducted to examine the occurrence of the enzymes, and their localization. Using enzymic, proteomic and/or tissue-specific transcriptomics. For this to operate in seagrasses it would have to take place mainly in the epidermal cells. Earlier studies (Abel and Drew 1989; Frost-Christensen and Sand-Jensen 1992), suggested that photorespiration rates were lower in seagrasses compared to the rates observed in terrestrial C3 plants. Recent work (Buapet et al. 2013) conducted on *Zostera marina* and *Ruppia maritima* provide contrasting evidence. These results suggest that photorespiration plays a significant role in these two species under increased pH and low dissolved inorganic carbon (DIC) concentrations. When comparing the seagrass species to the macrophytic green algae *Ulva intestinalis*, photosynthesis decreased significantly in higher pH, lower DIC conditions. This is not surprising, as *U. intestinalis* is known to have a CCM that can remove over half of the DIC from seawater in pH drift experiments (Maberly 1996). However, a similar extent of DIC removal has been found for some Australian seagrasses (Borum et al. 2016).

Whilst seagrasses are not generally so good at counteracting photorespiration compared to those algal counterparts that possess CCMs, we must also keep an open mind as to whether seagrasses possess the biochemical capability of the Mehler Ascorbate Peroxidase (MAP) pathway as has been observed in marine and other algae as well as in plants (Badger et al. 2000). This pathway intercepts hydrogen peroxide produced by the direct action of $O_2$ on the low potential reductants of PSI, producing superoxide, which finally generates two molecules of water (in the so-called water-water cycle). Hydrogen peroxide is also generated in the peroxisomes, during glycolate metabolism. More work is needed on the subject of seagrass photorespiration and the MAP pathway, as we still know very little about these processes. For example little is known about the type of catalase that exists in seagrass chloroplasts and peroxisomes. At present the only good evidence concerning photorespiration and the MAP pathway in seagrasses comes from *Halophila stipulacea* (Mass et al. 2010).

### *11.3.6 Photosynthetic Efficiency and Energy Down-Regulation*

Photosynthetic responses of seagrasses have been assayed mainly using fluorescence techniques in recent times although oxygen exchange and $^{14}C$ techniques have also been used and it is important that fluorescence techniques are calibrated against $O_2$ and DIC studies (see Larkum et al. 2006). Here we will deal mainly with recent Chl *a* fluorescence (Pulse Amplitude Modulation, PAM) techniques. However, mention should be made of the recent progress using vectorial, eddy correlation, oxygen techniques to measure oxygen exchange at the scale of seagrass meadows (without a chamber), so as not to impact the fluid dynamics of the mass flow through the meadow, which has highlighted many new insights (Rheuban et al. 2014a, b; Long et al. 2015); and of stable C-isotope techniques to measure carbon exchange processes in seagrasses (Hu et al. 2012; McPherson et al. 2015).

Seagrasses are nominally shade plants; that is, similarly to most benthic marine algae, they live beneath the surface of the ocean and live generally as shade plants, but nevertheless certain species can be exposed above water, and therefore be exposed and resistant to high light conditions (Petrou et al. 2013). This is in contrast to most land plants, which at one time or another have to sustain high light irradiances for substantial periods of time. Land plants evolved various mechanisms that deal with high light, the most common one being non-photochemical quenching (NPQ), the most common expression of which is the photo-protective xanthophyll cycle (see Larkum et al. 2006). This is a mechanism whereby the absorbed light energy, as excitation energy in chlorophylls is dissipated as heat before it can damage the reaction centre of Photosystem II. NPQ occurs in all seagrasses that have been studied (see next paragraph), although it is probably much less significant in deep-water species, as is the case for deep-water marine macroalgae (Runcie et al. 2008). It seems that most seagrasses have all the key enzymes necessary to carry out the xanthophyll cycle (Marín-Guirao et al. 2013; Olsen et al. 2016). A further point that needs to be made here is that seagrasses need a greater light intensity to survive at a given equivalent depth than many other hydrophytes (see Sect. 11.2.2). This either means that seagrasses have an inherent extra demand on energy assimilation, due to less efficient use of submarine irradiance and restricts them to shallower depths compared to freshwater hydrophytes or that the presence of epiphytes, which are common on seagrasses, causes an extra burden on their requirement for light in this way (see Sect. 11.5).

PAM studies have been carried out on a number of seagrasses and these all confirm the general hypothesis outlined above of shade-adapted plants that operate the xanthophyll cycle and other dissipative mechanisms in photoprotection under excess light (Ralph et al. 2002; Durako 2007; Bite et al. 2007; Campbell et al. 2008; Runcie et al. 2009; Horn et al. 2009; Collier et al. 2009; Mazzuca et al. 2013; Genazzio and Durako 2015).

## 11.4 Leaf Anatomy

Leaf anatomy has already been dealt with in great detail in Sect. 11.2.1. Here it is only necessary to remind the reader that the leaf anatomy of individual seagrass species can have a significant effect on overall photosynthesis and physiology. Seagrasses evolved in atleast three major families of plants (Chap. 1: the *Potamogetonaceae*, the *Hydrocharitaceae* and *Cymodoceaceae*, which are members of the subclass *Alismatidae*). These all inherited, as far as we know at present, the common features of seagrass leaves: a photosynthetic epidermis, much-reduced waxy cuticle, widespread aerenchyma and, with one generic exception in the case of the *Hydrocharitaceae*, strap shaped leaves with a basal meristem reinforced with xylem fibres, especially at the leaf base. The structure of the aerenchyma in seagrass leaves was examined in great detail in Larkum et al. (1989b). The genus *Halophila*, in the *Hydrocharitaceae*, has paddle-shaped leaves, which are petiolate

The strap shaped leaves of all seagrasses, except *Halophila* spp, leads on to the presence of seagrass algal epiphytes. The problems and effects of these algal epiphytes are dealt with in the next section.

## 11.5 Effect of Leaf Epiphytes on Seagrass Photosynthesis

Seagrass leaves can harbour a complex and diverse fouling community of bacterial biofilms (Sieburth and Thomas 1973), unicellular algae (Chung and Lee 2008), macroalgae (Lethbridge et al. 1988) and epiphytic invertebrates (Hughes et al. 1991). The role of leaf epiphytes on seagrass photosynthesis have been studied for decades (e.g. Sand-Jensen 1977; Brush and Nixon 2002) and while a few studies suggested a mutualistic relationship with nutrient exchange between epiphytes and seagrass leaves (Harlin 1973; McRoy and Goering 1974), the current belief is that epiphytes severely harm the seagrass through a range of factors.

First, light availability to the seagrass leaves is one of several key environmental factors regulating photosynthesis and thereby the fitness of the plant. Often, rooted macrophytes are spatially restricted to habitats that experience a minimum of 10% of surface irradiance (Borum 1983; Duarte 1991). In a recent study (Brodersen et al. 2015b), it was estimated that >90% of the incident irradiance can be attenuated by the epiphytic leaf community, thus leaving the seagrass <10% of surface irradiance. Furthermore, it was shown that not only the quantity of light changed but the spectral composition also changed towards a more green light-field (Brodersen et al. 2015b). The fractional absorption of green light (550 nm) by *Z. marina* is ~0.35 compared to a fractional absorption of ~0.65 in blue and red light (400–480 and 670 nm) (Cummings and Zimmerman 2003). Thus *Z. marina* is left with an increased fraction of light which is not effectively absorbed by its main light harvesting pigments, Chl *a* and *b* (Fig. 11.3).

Second, as well as the availability of light, the rate of photosynthesis can be limited by the supply of $C_i$ and efflux of $O_2$. The magnitudes of these processes are diffusion dependent (see Sect. 11.2.4) and thus regulated by the concentration gradient between the source and the sink, i.e. the water column and the seagrass leaf. However, the mass transfer is impeded by the DBL which surrounds all submersed surfaces, and the extent/thickness of the DBL is controlled by e.g. the surface topography and flow velocity; where a complex topography and low flow yields a thicker DBL. Brodersen et al (2015b) found that the leaf epiphyte-cover adversely affected the exchange of solutes across the DBL. With epiphyte cover the DBL thickness increased 4-fold, from ~350 µm to ~1400 µm, compared with epiphyte free leaves at a flow velocity of ~0.5 cm $s^{-1}$, thus impeding mass transfer of nutrients and dissolved gasses. Two of the major consequences of increased boundary layer thickness are: (1) In light, $O_2$ will build up around the seagrass leaves and increased $O_2$ concentrations can lead to enhanced photorespiration (Bowes and Ogren 1972; Dromgoole 1978; Mass et al. 2010). (2) In darkness, the passive $O_2$ supply from the water column is impeded by the thick boundary layer, which results in a ~75% reduction in $O_2$ concentration on the leaf surface in epiphyte covered leaves compared to bare leaves (and the same applies to uptake of N and P). The $O_2$ effect leaves the plant more vulnerable to sulphide intrusion via the roots, owing to inadequate internal aeration, and this has been identified as a key-factor in seagrass die-back events (Greve et al. 2003; Pedersen et al. 2004;

Borum et al. 2005; Brodersen et al. 2015a; Koren et al. 2015). Despite the increased $O_2$ concentrations in epiphyte-covered leaves, photosynthesis was lower than in epiphyte-free leaves. The compensation irradiance, i.e. the irradiance at which a positive net photosynthesis is just observed, was >2 times higher in epiphyte-covered leaves, thus leaving the plant for a longer period of the day in a negative energy balance (Fig. 11.3).

Epiphyte overgrowth have been correlated with nutrient over-enrichments (Borum 1983), and thus anthropogenic activities in coastal areas leading to increased nutrient loadings, through e.g. dredging and run-off, have the potential to affect the epiphytic overgrowth on seagrass leaves thus hampering plant fitness. Seagrass die-backs have a range of indirect effects such as sediment re-suspension, increased system respiration and increased sediment hydrogen sulphide concentrations (Burkholder et al. 2007) all potentially leading to declines in seagrass meadows.

## 11.6 Conclusions

Previous reviews (see e.g. Larkum et al. 2006) have dealt extensively with several topics and for this reason this chapter has dealt on a narrower range of topics. These are:

(a) the uptake of inorganic carbon by the leaves of seagrasses,
(b) the biochemistry of carbon fixation in photosynthesis,
(c) the influence of anatomy on photosynthesis and gaseous transport to the rhizome and roots, and,
(d) the effect of epiphytes on photosynthesis.

Of these four topics the one most extensively treated here is the first, the uptake of $C_i$ from the ambient seawater. This is because there are large lacunae in our knowledge of these processes, which are so profoundly important to our understanding of how seagrasses have become so successful in our seas over the last 100 million years and how today they are so important for the production of “blue carbon” (see Chap. 22). The second topic (b) is noteworthy because modern “omics” and direct profiling of genes and their products promises to throw light on a topic that has challenged research efforts over a long period. Nonetheless, if we were to mention some of the most important findings in seagrass photobiology since the previous review, they should include:

(i) that active $HCO_3^-$ uptake does not seem to occur across the plasmalemma.
(ii) that seagrasses utilize extracellular conversion of $HCO_3^-$ to $CO_2$, for enhanced $CO_2$ uptake and utilization in photosynthesis, e.g., through extracellular carbonic anhydrase (CA) activity.

(iii) the potential occurrence of a Carbon Concentrating Mechanism (CCM) in at least some seagrasses.
(iv) confirmation of shade-adaptation, and thus operation of the xanthophyll cycle and other dissipative mechanisms in photoprotection under excess light intensity.
(v) that leaf epiphytes can alter the spectral light composition towards a more green light-field, which is not as effectively absorbed by the main light harvesting pigments.

However, we will have to wait to see whether a C4-type of photosynthetic metabolism is eventually shown in seagrasses.

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# Chapter 12
# The Microbiology of Seagrasses

**J. R. Seymour, B. Laverock, D. A. Nielsen, S. M. Trevathan-Tackett and P. I. Macreadie**

**Abstract** Like both terrestrial plants and other benthic marine organisms, seagrasses host abundant and diverse communities of microorganisms. These microbes fundamentally influence seagrass physiology and health, while also regulating the biogeochemical dynamics of entire seagrass meadows. Discrete populations of bacteria, fungi, microalgae, archaea and viruses inhabit seagrass leaves, roots and rhizomes and the surrounding sediments. The plethora of ecological interactions taking place between seagrasses and this microbiome span the continuum of symbiotic relationships from mutualism to parasitism. Indeed, the metabolic activities of some seagrass associated microbes, such as diazotrophic and sulphur oxidizing bacteria, govern the local chemical environment in ways that facilitate seagrass survival. On the other hand, pathogens, such as the protozoan parasite *Labyrinthula* cause disease outbreaks that can lead to mass seagrass die offs. While the role of the seagrass microbiome in defining the success of seagrass habitats is becoming

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increasingly apparent, there is still much to be learnt. For instance, the development of an understanding of how seagrass associated microbes may buffer or augment the negative impacts of growing environmental pressures will be valuable for informing decisions regarding the management and conservation of threatened seagrass habitats. In this chapter we will synthesise the current state of knowledge on the microbiology of seagrasses, with a goal of conveying the often overlooked importance of the seagrass microbiome in governing seagrass health and the biogeochemical stability of seagrass ecosystems.

## 12.1 Introduction

It has been recognized for over 150 years that an intrinsic element in the health and growth of terrestrial vegetation involves the intimate ecological relationships between plants and microorganisms (Wainwright and Lederberg 1992; Gillings and Holmes 2004). Epiphytic, endophytic and rhizospheric microbes fundamentally shape the growth, condition and ecology of all land plants, and in turn have profound importance for the biological productivity of terrestrial ecosystems, agricultural processes, soil fertility and chemical cycling, and vegetation succession. Plant-microbe relationships include important mutualistic, commensal and pathogenic interactions. For instance, rhizobial bacteria fix nitrogen within the root nodules of their symbiotic plant partner, providing many plant species with an essential source of bioavailable nitrogen (Peoples et al. 1995), while mycorrhizal fungi play pivotal roles in enhancing nutrient and water absorption in host plants (Bolin 1991). On the other hand, a diverse assortment of microorganisms, including viruses, bacteria, fungi and protozoa, are significant plant pathogens, causing either death or significant decreases in the growth and productivity of both natural plant populations and agricultural crops (Fegan and Hayward 2004).

The delicate balance between the influence of beneficial and pathogenic microbes has undoubtedly shaped plant evolution (Chisholm et al. 2006), and it is now widely appreciated that plant fitness is not only a consequence of the plant itself, but also its resident microbiota (Vandenkoornhuyse et al. 2015). Although there are many physiological and ecological differences between terrestrial and marine plants, there is evidence that marine plants, including the seagrasses, will have similar ecological bonds to microorganisms. However, relative to the highly developed understanding of terrestrial plant-microbe interactions, which has largely been provided by agricultural science, our understanding of the microbiology of seagrasses is incipient.

Significant seagrass-microbe interactions are likely because microorganisms are a dominant biotic feature across all marine ecosystems. A typical milliliter of seawater contains around 1 million bacteria and an order of magnitude more viruses, while marine surface sediments can contain between 100 million to 1 billion bacteria per gram (Whitman et al. 1998). Across the entire ocean, microorganisms are estimated to account for up to 90% of all biomass

(Amaral-Zettler et al. 2010). These microbes are also incredibly diverse, with a single liter of seawater containing up to 20,000 different bacterial species (Sogin et al. 2006). Since the development of methods to accurately quantify marine microorganisms during the 1980s (Porter and Feig 1980) and the advent of molecular microbiological and genomic approaches during the 1990s–2000s (Fuhrman and Ouverney 1998; DeLong et al. 2006), the fundamental trophic and biogeochemical roles of marine microorganisms have been revealed (DeLong and Karl 2005; Falkowski et al. 2008; Seymour 2014). An emerging research focus has since been centered on the ecological relationships between these microbes and marine animals and plants (Taylor et al. 2007; Egan et al. 2013).

Macroorganisms inhabiting both the pelagic and benthic realms of the ocean host dense microbial communities, which include both beneficial symbionts (McFall-Ngai 2014; Ainsworth et al. 2015) and disease-causing pathogens (Ben-Haim and Rosenberg 2002). The recent increased interest in the interactions between marine microbes and their animal or plant hosts has occurred in parallel with the emergence of two biological concepts that have begun to fundamentally re-shape our perception of the relationships between macro- and microorganisms, namely the notions of the *Microbiome* and the *Holobiont*. A microbiome is defined as the collection of all of the microorganisms living in association with an organism, and there has been a growing realization that the overall composition and function of an organism's microbiome fundamentally influences the health of the host organism (Eloe-Fadrosh and Rasko 2013). Related to this, the holobiont, or whole unit of life (Margulis 1991), is the view that every organism (biont) lives in multiple symbiotic relationships with a consortia of other organisms, including members of its microbiome, and that these symbiotic partners represent an integrated community that is essential for each members survival (Margulis 1991).

The Holobiont concept has been applied to a range of benthic marine organisms, in particular corals, where this term was first widely endorsed and popularized (Rohwer et al. 2002). The 'coral holobiont' model has clearly demonstrated that the health of corals is strongly mediated by the composition and function of the coral host's symbiotic microbial partners, with evidence that environmental stress can lead to a dysbiosis among the coral microbiome, whereby beneficial microbes are outcompeted and replaced by pathogenic bacteria, to the detriment of the coral host (Vega Thurber et al. 2009; Tout et al. 2015). The 'seaweed holobiont' has also been examined within the context of marine macroalgae, with evidence for a tight mutualistic link between the host macroalgae and epiphytic bacteria, which have been shown to be essential for development of the algal host and to release chemicals that protect the host from detrimental colonization by other epibiota (Egan et al. 2013). The holobiont concept has also been applied to terrestrial plants (Vandenkoornhuyse et al. 2015), but while likely to be highly germane to seagrass ecology and physiology, the idea of a seagrass holobiont has not yet been explored.

Our current knowledge of seagrass microbiology points towards several fundamentally important ecological links between the seagrass 'host' and its resident and spatially proximal microorganisms. This is consistent with patterns observed among both terrestrial plants (Berg et al. 2014) and other benthic marine organisms

(Rohwer et al. 2002; Taylor et al. 2007; Egan et al. 2013). Seagrasses directly benefit from a number of microbiological processes, including the activities of symbiotic heterotrophic diazotrophic bacteria, which fix nitrogen within the rhizosphere and thereby enhance seagrass productivity (Welsh 2000). Alternatively, other microbial activities, such as the production of elevated levels of toxic hydrogen sulphide by sulphate reducing bacteria (Carlson and Forest 1982) or infection by disease causing protists (Ralph and Short 2002), can have detrimental impacts on seagrass health. Notably, as has been observed in other benthic organisms (Vega Thurber et al. 2009; Tout et al. 2015), the balance of these beneficial and detrimental relationships with microbes can be tipped as a consequence of environmental stress associated with processes such as eutrophication or global warming (Garcia et al. 2013). From the perspective of a microorganism, seagrasses provide a habitat rich in organic carbon and a diversity of suitable chemical microenvironments (Devereux 2005), providing strong motivation to inhabit plant surfaces, the rhizosphere or surrounding sediments. Finally, at an ecosystem level, interactions between seagrasses and microorganisms can directly influence large-scale biogeochemical processes, including coastal carbon sequestration (Fourqurean et al. 2012; Macreadie et al. 2015). Given the significance and diversity of microbial influence, it is clear that microbiological parameters should have prominence within most examinations of seagrass ecology.

Our current understanding of seagrass microbiology has been derived from a combination of culture based (Nielsen et al. 1999) and culture independent techniques (Jensen et al. 2007), as well as process-based studies (e.g. bacterial production and respiration rates) (Moriarty et al. 1985; Pollard and Moriarty 1991). Relative to other analogous marine systems, such as corals and seaweeds, the uptake of modern molecular microbiological and ecogenomic approaches has arguably been slower within the study of seagrass biology, but is beginning to build momentum. Such a technical and conceptual step-change will be necessary to build a microbiome-based approach to examining seagrass ecology. In this chapter, we will consider seagrass-microbe interactions from several perspectives, including treatises on the key groups of seagrass associated microbes and their ecological functions, the microbial habitats and microenvironments associated with seagrasses, the influence of pathogenic microbes, and the roles of seagrass associated microbes in both localised chemical cycling and large-scale biogeochemical processes. Due to a scarcity of microbiological data from Australian seagrass habitats, rather than solely focusing on the Australian seagrass ecosystems that are the subject of this book, we will provide a generalised treatment of seagrass microbiology, spanning different seagrass species and geographical regions, with some reference to Australian research in this space.

## 12.2 Important Microbes Within Seagrass Ecology

Seagrasses provide a number of potential colonizable microhabitats for diverse populations of microorganisms that can assume mutualistic, saprophytic, parasitic or pathogenic roles (Fig. 12.1). To date the microbiological characterisation of seagrasses has been largely biased towards examinations of bacterial populations, but if lessons are learnt from other benthic host-microbe systems, it is probable that members of all three domains of life, as well as viruses, will play important ecological roles within the seagrass holobiont.

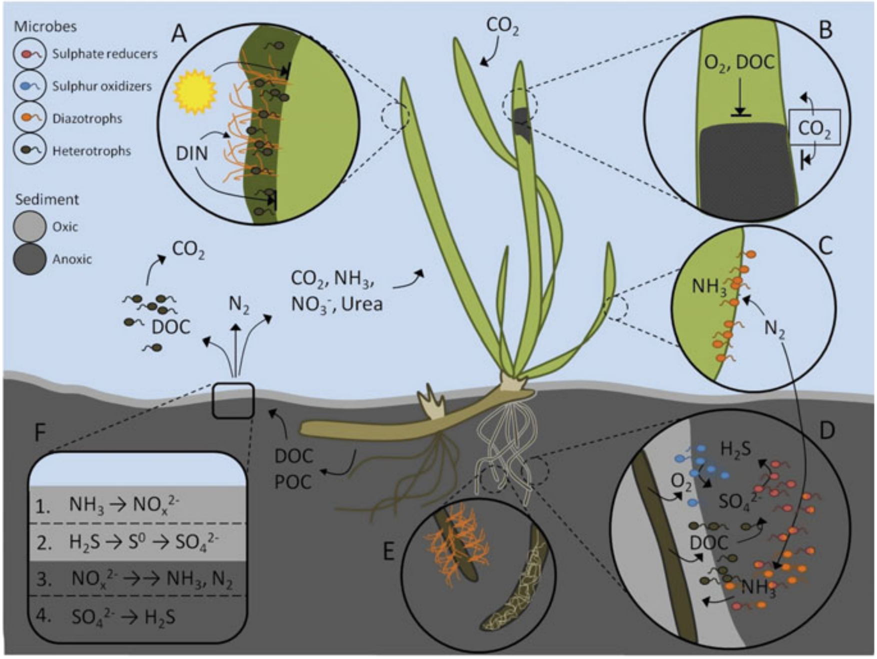


**Fig. 12.1** Conceptual diagram of key segrass-microbe interactions. *Inset A* Leaf epiphytic growth of algae, fungi and heterotrophic microbes resulting in lowered incident irradiance and access to dissolved inorganic nitrogen (DIN) from the water-column. *Inset B* Wasting decease lesion (grey) caused by *Labyrinthula*, limiting carbon fixation and transport of oxygen and dissolved organic carbon to the rhizome and roots. *Inset C* Leaf associated nitrogen fixing microbial biofilm (orange) facilitating nitrogen uptake through the leaves. *Inset D* Oxygen and dissolved organic carbon (DOC) released from the plant drive microbial processes including sulphur cycling and nitrogen fixation in the root and rhizosphere microenvironment. Inset E: Bacterial and fungal epiphytes on seagrass roots. Inset F: Important microbial processes in the seagrass sediment driving nutrient cycling and carbon turnover; (1) Nitrification, (2) Sulphide oxidation, (3) Denitrification, Nitrate reduction and Dissimilatory nitrate reduction to ammonia (DNRA), (4) Sulphate reduction

### *12.2.1 Bacteria*

Consistent patterns in bacterial biomass, whereby abundances are substantially elevated in association with seagrasses, provide initial evidence for an important ecological relationship between seagrasses and bacteria. Abundances of epiphytic bacteria on seagrass leaves are significantly higher than seawater concentrations (Kirchman et al. 1984), and similarly seagrass sediments host substantially higher bacterial abundances than adjacent bare sediments (Duarte et al. 2005). These elevated bacterial cell densities occur as a consequence of bacterial utilisation of the large quantitates of dissolved and particulate organic carbon released from seagrasses (Pollard and Moriarty 1991; Kaldy et al. 2006). Therefore, it is not surprising that patterns in bacterial activity generally reflect biomass patterns, whereby, relative to unvegetated sediments and the adjacent water column, rates of bacterial production, respiration, sulphate reduction, denitrification and nitrogen fixation are all elevated within seagrass rhizomes and sediments (Capone 1982, 1983; Moriarty et al. 1985; Pollard and Moriarty 1991; Williams et al. 2009; Eyre et al. 2011). Collectively, these abundant and active bacterial communities are the dominant consumers of seagrass primary production (Mann 1998) and play essential roles in promoting seagrass productivity via nutrient recycling processes (Welsh et al. 2000), but it is important to note that seagrass associated bacterial assemblages are highly diverse with multifarious ecological and biogeochemical roles, meaning that they should not be considered a single or homogenous entity.

Early examinations of bacterial diversity within seagrass habitats employed culture-dependent approaches, resulting in the isolation of several novel, potentially seagrass-specific, bacterial species (Nielsen et al. 1999; Shieh et al. 2000; Yoon et al. 2007). While molecular approaches are yet to be exploited as widely as in other ecosystems, a handful of studies have targeted the bacterial 16S rRNA gene using community finger-printing, clone library and amplicon sequencing approaches within seagrass habitats. These studies have demonstrated that seagrasses host bacterial communities that differ to those associated with other marine plants (Crump and Koch 2008), and while there is some evidence for dissimilarities between bacterial communities associated with different seagrass species (Uku et al. 2007), a number of apparently universal patterns have been observed.

Epiphytic bacterial assemblages are typically dominated by aerobic heterotrophs from the α- and *γ-Proteobacteria*, along with *Flavobacteria, Bacteroidetes* and *Cyanobacteria* (Weidner et al. 2000; Uku et al. 2007; Crump and Koch 2008; Hassenruck et al. 2015). Among these, aerobic heterotrophs from several major marine genera including *Vibrio*, *Pseudoalteromonas, Oceanospirillum, and Roseobacter* are recurrent members of seagrass epibiota. On the other hand, sediment and root microenvironments are characterised by very different bacterial communities, and are typically dominated by sulphate reducing bacteria from the *δ–Proteobacteria,* and sulphur oxidizing bacteria from the *γ-Proteobacteria* and *ε-Proteobacteria* (Cifuentes et al. 2000; Jensen et al. 2007). Notably, there is evidence for further spatial partitioning of these groups, with roots hosting a higher proportion of potentially symbiotic $\gamma$-*Proteobacteria* and $\varepsilon$-*Proteobacteria* and nearby sediments containing more sulphate reducing bacteria. These patterns in bacterial diversity across the seagrass holobiont are clearly linked to the ecological and functional niches filled by bacterial populations associated with different chemical and oxic microenvironments. While there is evidence for substantial diversity among seagrass-associated bacterial communities (Hassenruck et al. 2015), within the context of seagrass ecology and physiology, the three most significant functional groups of bacteria are arguably the aerobic heterotrophs, sulphate reducing bacteria and diazotrophic (nitrogen fixing) bacteria.

Bacterial communities inhabiting the surfaces of seagrass leaves, the rhizosphere and the upper few millimeters of sediment generally experience oxic conditions. The aerobic bacteria inhabiting these environments are typically highly active, characterised by high levels of production and comprised of heterotrophic bacterial groups (e.g. $\alpha$- and $\gamma$-*Proteobacteria*) that are ubiquitous within seawater environments. Aerobic heterotrophs inhabiting the oxic zone that extends a few hundred micrometers from seagrass roots will gain first access to the labile organic substrates exuded into the rhizosphere (Devereux 2005). Within the surrounding sediments, while restricted to a relatively narrow surface layer and generally occurring in substantially lower abundance than anaerobic bacteria, aerobic heterotrophs are responsible for a significant fraction of organic matter decomposition and therefore play an important role in both carbon cycling and nutrient remineralization processes (Moriarty et al. 1985).

Below a few millimeters under the sediment surface, oxygen penetration is minimal and anaerobic bacterial metabolisms dominate. In marine sediments sulphate is the most available terminal electron acceptor (Capone and Kiene 1988), and sulphate reducing bacteria, which oxidize organic substrates while reducing sulphate to hydrogen sulphide, are responsible for up to 50% of organic material remineralization (Jørgensen 1982). Within seagrass sediments sulphate reducing bacteria, primarily belonging to the $\delta$–*Proteobacteria,* are among the most abundant bacterial group (Cifuentes et al. 2000) and play fundamental roles in carbon and nutrient cycling (Devereux 2005). Notably, the by-product of sulphate reducing bacterial activity, hydrogen sulphide ($H_2S$), is a potent phytotoxin that has been shown to inhibit seagrass growth and photosynthesis and has been implicated as a causative agent in seagrass declines (Holmer and Hassler-Sheetal 2014).

Due to their role in producing toxic $H_2S$, it is somewhat paradoxical that sulphate reducing bacteria in fact provide valuable services to seagrasses, and may even be considered important symbiotic partners. The activities of sulphate reducing bacteria can help to maintain sediment geochemical conditions appropriate for seagrass growth (Pollard and Moriarty 1991), but perhaps more importantly, many sulphate reducing bacteria are also diazotrophs (Welsh 2000), meaning that they have the capacity to fix biologically unavailable dinitrogen gas ($N_2$), into ammonium ($NH_4^+$). Nitrogen fixation is an important process within seagrass habitats, where nitrogen availability can place substantial limits on primary production (Patriquin 1972). Indeed, diazotrophic bacteria provide seagrasses with up to 65% of their nitrogen requirements (Welsh 2000; Devereux 2005). While some cyanobacterial diazotrophs live in association with seagrasses (Lyimo and Hamisi 2008), the bulk of diazotrophic activity comes from heterotrophic bacteria (Welsh 2000), with up to 95% of nitrogen fixation attributed to sulphate reducing bacteria (Capone 1982). The mutualistic partnership between seagrasses and sulphate reducing bacteria may be further facilitated by the co-occurrence of sulfur oxidizing bacteria from the ε-*Proteobacteria* including *Sulfurimonas* and *Thiomicrospira*, which inhabit seagrass roots and detoxify the surrounding sediments by oxidizing the $H_2S$ generated by the sulphate reducing bacteria (Jensen et al. 2007). These multifaceted inter-species interactions are indicative of a complex and highly interconnected microbiome, involving synergistic relationships between the seagrass and multiple bacterial partners.

### *12.2.2 Fungi*

The symbiotic associations between terrestrial plants and fungi represent one of the oldest and most widespread symbioses (Pirozynski and Dalpé 1989; Remy et al. 1994; Gianinazzi-Pearson 1996). Up to 90% of land plants are believed to rely on fungal symbiotic partners (Bonfante and Genre 2010). While both epiphytic and endophytic fungi occur in most plants, the most important plant symbionts are the mycorrhizal fungi, which live in association with plant roots and play an essential role in facilitating plant nutrient assimilation and protection from pathogens (Smith and Read 2008).

Although largely overlooked for many years, fungi are now known to occur ubiquitously in marine environments (Hyde et al. 1998). It has been recognised since the 1840s, when fungi were first reported in the rhizome of *Posidonia oceanica* (Vohnik et al. 2015), that fungi live in association with seagrasses. However, because seagrasses are believed to assimilate a substantial proportion of their nutrients through the leaves rather than the roots (Stapel et al. 1996), it has been proposed that they might lack mycorrhizal symbionts (Vohnik et al. 2015), and indeed Nielsen et al. (1999) were unable to find any evidence for arbuscular mycorrhizal fungi associated with the seagrass species *Zostera marina* and *Thalassia testudinum,* which they attributed to the inhibitory effects of low oxygen levels and high salinity in seagrass sediments. On the other hand, endophytic fungi have been observed in both the leaves and rhizomes of several seagrass species, but both the abundance and diversity of seagrass associated fungal communities appear to be much lower than is observed in terrestrial plants (Devarajan et al. 2002; Shoe-maker and Wyllie-Echeverria 2013; Venkatchalam et al. 2015).

It is notable that across a number of seagrass species, a relatively narrow range of fungal endophytes have been identified, with members of the Ascomycota, primarily *Aspergillus* and *Penicillium* species, typically the dominant fungal endophytes (Shoe-maker and Wyllie-Echeverria 2013; Venkatchalam et al. 2015). Ascomycota have also been shown to be the dominant fungal group in the sediments surrounding the seagrass *Enhalus acoroides* (Ling et al. 2015). The dominance of these fungi across a broad range of seagrass species and geographic regions is indicative of a potentially important ecological role of these groups within seagrass habitats (Venkatchalam et al. 2015). Members of the *Aspergillus* and *Penicillium* genera are commonly soil-dwelling saprophytes that utilise plant derived organic substrates (Grantina-Levina et al. 2013), perhaps implying a largely saprophytic, rather than symbiotic function among the most dominant seagrass associated fungi. A potential exception to this pattern however, is a recently described dark septate endophytic (DSE) association observed in the roots of *Posidonia oceanica* (Vohnik et al. 2015). DSE are common colonizers of terrestrial plant roots, where they typically play beneficial roles that ultimately enhance plant shoot and root biomass (Newsham 2011). The DSE identified within the roots of *P. oceanica* have been identified in *P. oceanica* populations spanning a broad geographic area, providing initial clues for a potentially significant symbiotic relationship between DSE and seagrasses (Vohnik et al. 2015).

While the consistent observation of seagrass-associated fungi points towards a potentially important role of fungi within seagrass physiology and ecology, our current understanding of seagrass mycology is largely derived from culture dependent and microscopic approaches, and clear insights into the ecological functions of seagrass-associated fungi are lacking. The application of next generation sequencing approaches targeting fungal specific 18S rRNA genes and internal transcribed spacer (ITS) regions are likely to yield much deeper insights into the diversity and functional dynamics of seagrass associated fungal communities.

### *12.2.3 Protozoa*

Diverse populations of autotrophic and heterotrophic protozoa live in epiphytic and endophytic associations with seagrasses (Michael et al. 2008). Among these, photosynthetic microalgae are among the most abundant and ecologically important epiphytes on seagrass leaves (Frankovich and Zieman 1994). Epiphytic microalgae have ecosystem-level significance within seagrass habitats by providing a dominant fraction of the carbon ultimately transferred into the foodweb by herbivory, and playing important roles in nutrient cycling processes (Moncreiff and Sullivan 2001). Notably, the photosynthetic production of these microalgae can often rival or exceed seagrass production, meaning that epiphytic algae substantially enhance the overall productivity of seagrass habitats (Moncreiff and Sullivan 2001). Members of the red, brown and green algae colonize the surfaces of seagrass leaves, but diatoms, along with cyanobacteria, are typically the most numerically and ecologically relevant epiphytes (Chung and Lee 2008). Diverse assemblages of diatom species preferentially colonize seagrass surfaces relative to other available substrata (Jacobs and Noten 1980; Pinckney and Micheli 1998; Chung and Lee 2008), while small diatoms also dominate the microalgal biomass in sediments surrounding seagrasses (Daehnick et al. 1992).

In addition to the provision of a suitable colonisable surface within an optimum light environment, seagrass hosts also provide epiphytic microalgae with enhanced access to nutrients (Harlin 1975). From the perspective of the seagrass host, epiphytic microalgae can have both beneficial and detrimental effects. When microalgal densities become too high, as a consequence of environmental perturbations including eutrophication (Mateo et al. 2007), seagrass photosynthesis and growth can be inhibited due to shading effects (Sand Jensen 1977). Furthermore, dense populations of epiphytic microalgae can decrease diffusion of $CO_2$ and nutrients to the host (Michael et al. 2008) or outcompete the seagrass host for nutrients (Lobelle et al. 2013). On the other hand, epiphytic microalgae may in certain circumstances benefit the seagrass host by providing UV protection or reducing desiccation stress in shallow water or habitats that temporarily experience aerial exposure (van Montfrans et al. 1984). As with many holobiont systems, the balance of these positive and negative interactions is likely to shift as a consequence of both the host's health status and the influence of environmental stressors, and there is also evidence that the seagrass host may actively promote colonisation by potentially beneficial epiphytes (Pinckney and Micheli 1998).

Heterotrophic protozoa are also likely to play an important role within the ecology of seagrass habitats. Epiphytic heterotrophic flagellates and ciliates inhabit seagrass leaves (Neckles et al. 1994; Aladro-Lubel and Martinez-Murillo 1999) and graze upon bacterial and microalgal epiphytes (Peduzzi and Herndl 1991). Because grazing by heterotrophic protists not only influences bacterial and microalgal abundance, but community composition (Jürgens and Massana 2008), the activities of these heterotrophic protozoa may fundamentally shape the microbiology of seagrass surfaces. Another notable protist within seagrass ecology, which is discussed in detail later in this chapter, is *Labyrinthula zosterae*, the causative agent of seagrass Wasting Disease, which has resulted in a number of major seagrass die-offs in the Northern Hemisphere (Muehlstein 1989). Evidence that *Labyrinthula* is omnipresent even in healthy seagrass meadows (Vergeer and den Hartog 1994), but becomes pathogenic under certain environmental conditions or seagrass health states is analogous to other benthic holobiont systems, where specific members of the microbiome can opportunistically assume a parasitic or pathogenic state under stress conditions (Tout et al. 2015).

### *12.2.4 Archaea*

While the *Archaea* are now known to occur within all marine environments (DeLong 1992, Fuhrman et al. 1992) and not just in the extreme habitats where they were originally identified, there is so far little evidence for seagrass-archaeal interactions. Although, this could simply be due to a paucity of research in this area. Among terrestrial plants there is recent evidence that archaea can sometimes represent a significant proportion (36%) of prokaryotic endophytes, implying a potentially important symbiotic role (Müller et al. 2015). Marine archaea are important symbiotic partners for a range of benthic organisms including sponges, where they are thought to play an important role in ammonia oxidation (Zhang et al. 2014). Trias et al. (2012) observed ammonia oxidizing archaea (AOA) on the surfaces of marine macrophytes, including members of the red and brown macroalgae. However, a notable observation from that work was that unlike nearly all other marine environments, the abundance of AOA was lower than bacterial ammonia oxidizers, perhaps implying a lower relative importance of AOA within this microhabitat. Archaea are abundant in marine sediments (Lloyd et al. 2013), and one of the few studies to so far examine the potential for seagrass-archaea associations revealed the existence of both *Euryarchaetoa* and *Crenarchaeota* populations in the sediments associated with *Zostera noltii* (Cifuentes et al. 2000). Yet, little is currently known about the potential ecological and biogeochemical significance of these seagrass associated archaea communities and a more widespread application of next generation sequencing approaches within seagrass habitats is required to elucidate the significance of the domain *Archaea* in seagrass ecology.

### 12.2.5 Viruses

Viruses are the most abundant and geographically ubiquitous biological entities in the ocean. While the majority of marine viruses are bacteriophage (Suttle 2007), viruses specific to a wide range of animal and plant hosts have been identified within the marine environment (Munn 2006). Marine viruses have significant ecological impacts for a number of benthic organisms, including macroalgae, where they potentially have substantial ecological and evolutionary significance among seaweeds (Egan et al. 2013). Seaweed viruses infect free-living gametes and spores as well as seaweed tissues (Van Etten et al. 2002) and it has been demonstrated in some seaweed species that as much as 50% of the population can be infected by viruses (Cock et al. 2010). However, there is as yet no conclusive data indicating the occurrence of viruses in the tissues of seagrasses, but as with the *Archaea* this may simply be due to a lack of research in this area. A study by Luna et al. (2013) demonstrated significantly higher abundances ($>2 \times 10^9$ g$^{-1}$) of viruses and virus: bacteria ratios in sediments surrounding the seagrass *Posidonia oceanica* than in un-vegetated sediments. While viruses inhabiting the sediments are perhaps unlikely to be infective agents of seagrasses, sediment viruses are responsible for bacterial mortality (Glud and Middelboe 2004), which may indirectly influence sediment chemistry and seagrass health by altering sediment bacterial community composition. By increasing dissolved organic carbon pools through the lysis of bacterial cells (Wilhelm and Suttle 1999), viruses may also influence carbon budgets within seagrass sediments.

### *12.2.6 Role of Seagrasses in Controlling Their Microbiome*

It is becoming clear that the fitness of most, if not all, macroorganisms relies on the beneficial functions provided by a healthy microbiome (Schreiner et al. 2015), and there is evidence that host organisms can directly manipulate the composition of their microbiome to their advantage (Reshef et al. 2006). An important strategy in this manipulative management of the microbiome is likely to be the release of selective metabolites that promote the growth of beneficial microbial partners or restrict the growth of detrimental microbes. Seagrasses appear to have this capacity.

In addition to chemical defences such as phenols, caspases and reactive oxygen species, some species of seagrass have been shown to produce antibiotic compounds that directly protect against microbial colonisation (Cariello et al. 1979; Jensen et al. 1998; Bushmann and Ailstock 2006; Engel et al. 2006), suggesting that the plant is able to influence the composition of attached microbial communities. Recent investigations have also revealed similar properties in some of the fungal endophytes associated with the seagrasses *Cymodocea serrulata*, *Halophila ovalis* and *Thalassia hemprichii*. Endophytic fungal isolates from all three seagrass species exhibited strong antifungal properties against pathogenic yeasts (e.g. *Candida albicans*) and filamentous fungi (e.g. *Penicillium marneffei*), as well as antimicrobial activity against bacteria, including the human pathogens *Staphylococcus aureus* and *Pseudomonas aeruginosa* (Supaphon et al. 2013). Screening of the seagrass *Enhalus acoroides* for epiphytic and endophytic bacteria suggested that endophytic species in particular may offer some protection against biofilm-forming bacteria (Marhaeni et al. 2010), raising new questions about how the different parts of the seagrass holobiont interact with each other.

## 12.3 Microbial Habitats Associated with Seagrass

The multifaceted ecological interactions between seagrasses and their associated microbiota are played out within a variety of microniches associated with different parts of the plant and the nearby sediments (Fig. 12.1). These discrete microenvironments support specific microbial assemblages adapted to the prevailing physical and chemical conditions. The distinct microbial assemblages inhabiting these niches perform an array of functions that can either positively or negatively impact the seagrass host. In this section we consider the key microenvironments within seagrass meadows and review our current understanding of the microbial communities inhabiting them.

### 12.3.1 Leaves

Seagrass leaves play host to a diverse community of microbes including epiphytic bacteria (Wahbeh and Mahasneh 1984; Shiba et al. 1991; Uku et al. 2007; Crump and Koch 2008), fungi (Sathe and Raghukumar 1991; Panno et al. 2013) and protists (Vergeer and den Hartog 1994; Garcias-Bonet et al. 2011). These epiphytic microbes likely interact with each other as well as with the seagrass host and algal epiphytes, however in-depth understanding of these interactions within the leaf microbiome is still lacking. Recent advances in microscopy, cytometry and molecular biology have improved our knowledge of bacterial abundances and community composition on seagrass leaf tissues (Trevathan-Tackett et al. 2014; Torta et al. 2015). Bacteria are the most abundant microbial colonizers with cell counts reported in the ranges of $10^1$–$10^{14}$ cells $cm^{-2}$ (Kirchman et al. 1984, Novak 1984; Kurilenko et al. 2001; Williams et al. 2009) or $10^5$–$10^8$ cells $g^{-1}$ FW (Wahbeh and Mahasneh 1984; Shiba et al. 1991). Bacterial densities have been shown to shift seasonally with abundances peaking in the summer months coinciding with higher photosynthetic production as well as changes in the production of anti-microbial compounds (Wahbeh and Mahasneh 1984). This summer community has been shown to be dominated by *Arthobacter*, *Actinomycetes* and *Bacillus*, with a shift to *Pseudomonas*- and *Vibrio*-dominated communities in the winter (Wahbeh and Mahasneh 1984).

Densities and spatial distributions of epiphytes on a leaf may also depend on antagonistic interactions and competition with other bacteria, diatoms or macroalgae (Novak 1984 and references therein), as well as age of the leaf. Bacteria have been shown to promote leaf growth of seagrass seedlings by providing beneficial metabolites and nutrients as well as controlling epiphytic algae growth (Celdran et al. 2012). On young leaves, bacteria remain epiphytic with no penetration of the leaf epidermis (Kuo 1978). However, once the leaf begins to age, bacterial densities increase, particularly at the leaf tips (Kirchman et al. 1984; Barnabas 1992). Even prior to senescence and detachment, bacteria begin to invade and decompose older leaf tissues, likely with the aid of cellulose-degrading enzymes that degrade the cell wall (Barnabas 1992).

Much of what is known about the function of epiphytic microbes comes from studies on autotrophic and heterotrophic bacteria, many of which form a mutualistic or symbiotic relationship with seagrass at the scale of an individual leaf. For example, heterotrophic epiphytic microbes utilise photosynthate excretions of seagrasses (Hough and Wetzel 1975, Kirchman et al. 1984) and in return provide up to a third of a seagrass nitrogen demand through nitrogen fixation (Capone and Taylor 1977, 1980; Cole and McGlathery 2011). Epiphytic microbes also support meadow-wide functions including supporting nearby benthic bacterial C demands (Williams et al. 2009), supporting food webs by providing food for grazing isopods and amphipods (Neckles et al. 1993, 1994) and providing the majority of total nitrogen in a seagrass meadow via nitrogen fixation (Cole and McGlathery 2011). Microbes play important roles in nutrient cycling across seagrass meadows due to their capability to degrade seagrass leaves beginning at senescence (see 4.1 section for more detail). For example, some bacteria (i.e., *Cytophagia*, *Lewinella*) and fungi (i.e., *Flavodon flavus*) produce polymer-degrading enzymes, which breakdown refractory structural carbohydrates (e.g., lignocelluloses) found in seagrass tissues (Sathe and Raghukumar 1991; Raghukumar et al. 1999; Crump and Koch 2008; Mtui and Nakamura 2008; Panno et al. 2013).

While there is the potential for epiphytic microorganisms to invade live seagrass leaves, seagrasses are rich in phenolic compounds (Zapata and McMillan 1979; Arnold et al. 2008), which can help control biofouling and microbial invasions (Harrison 1982b). For example, crude extracts from seagrass have been shown to be active against saprobic fungi and protists as well as pathogenic bacteria and protists (Jensen et al. 1998; Puglisi et al. 2007; Ross et al. 2008; Trevathan-Tackett et al. 2015). However, as a result of ageing, the concentration and potency of the anti-microbial compounds produced by seagrasses becomes diminished (Harrison 1982a; Ravn et al. 1994) allowing for invasion of aged tissues (Barnabas 1992). Additionally, if healthy leaves are damaged by physical disruption, such as those caused by leaf-burrowing isopods in the leaves of *Posidonia australis*, the damage can facilitate invasion of bacteria and fungi into the leaf and even cause localised necrosis on the leaf (Brearley and Walker 1995).

Despite evidence for their role in seagrass decomposition, the information on the abundances and community profiles of eukaryotic microbes living on seagrass leaves is much sparser compared to their prokaryotic counterparts. Fungal densities have been estimated at $10^2$ colony forming units $g^{-1}$ DW (Panno et al. 2013), while protist cells have been shown to range from 0.01 to 504 cells $mg^{-1}$ DW (Bockelmann et al. 2013). However, the information on eukaryotic epiphytic taxa is still growing. For example, the identification of epiphytic protists, like *Labyrinthula*, are mostly limited to microscopy-based studies or culturing approaches (Muehlstein et al. 1988; Porter 1990; Muehlstein et al. 1991), though analyses using targeted ITS regions has recently become more prevalent (Garcias-Bonet et al. 2011; Bockelmann et al. 2013). Panno et al. (2013) recently identified 20 species of fungi isolated from *Posidonia oceanica* leaves, with observed fungal concentrations higher than found on algae, sponges or corals. Many fungal taxa from the division of Ascomycota have been isolated from seagrass leaves for purpose of natural product research (Belofsky et al. 1999; Kasai et al. 2005; Arunpanichlert et al. 2011, 2012; Afiyatullov et al. 2015; Arunpanichlert et al. 2015a, b). While our knowledge of epiphytic microbial communities and functions has expanded in the last couple of decades, there is still a paucity of data concerning eukaryotic epiphytes. Increased application of molecular biological approaches will further our understanding of the composition and function of epiphytic microbes in seagrass meadows.

### 12.3.2 Internal Tissues

Seagrasses contain large populations of microbial endophytes, defined as any microorganism inhabiting the internal plant tissues whose presence is, at least transiently, not harmful to the plant (Schulz and Boyle 2006). The endobiont may therefore contain organisms that display latent pathogenicity, which may become apparent under certain life stages or environmental conditions, as well as symbiotic microorganisms with beneficial roles for the plant (Schulz and Boyle 2006). Bacteria, archaea and fungi have been found colonizing the internal tissues of seagrass roots, stems and leaves. The identity of these endophytes raises intriguing questions about their functional interactions with the plant.

Bacteria may passively colonize seagrass tissues via root junctions or wound sites in response to the radial loss of oxygen or labile organic carbon (DOC) (Devereaux 2005; Schulz and Boyle 2006), although some bacteria in seagrass root tissues also appear able to lyse outer cell walls (Kuo 1993). Microbial cells have been observed penetrating the outer cortical cells of the roots of four different species of tropical seagrass (*Thalassia hemprichii*, *Cymodocea serrulata*, *Halodule uninervis*, *Syringodium isoetifolium*) (Kuo 1993). Sulphate-reducing bacteria, unidentified archaea and the acetogenic isolate *Clostriudium glycolicum* were all found within the deep cortical cells of *Halodule wrightii* (Küsel et al. 1999, 2001). Subsequently, a sulphate reducing bacterium, *Desulfovibrio zosterae* and a new sulfite-oxidising bacterium, *Sulfitobacter delicatus* were isolated from surface-sterilised roots and tissue homogenate, respectively (Nielsen et al. 1999a; Ivanova et al. 2004). The endophytic bacteria in seagrass root tissues therefore bear some resemblance to those within surrounding anoxic sediments and indeed appear to be organised according to oxygen gradients, with the sulphate reducing bacteria occupying tissues closest to the root centre, and the acetogenic bacteria and archaea occurring mostly in the rhizoplane and outer cortex.

Leaf and stem tissue endophytes have received less attention than those inhabiting root and rhizome tissues. Garcias-Bonet et al. (2012) detected prokaryotic DNA in >80% of the tissues studied within Mediterranean *Posidonia oceanica* meadows (roots, rhizomes and leaves). The associated Operational Taxonomic Units (OTUs) mostly belonged to the *Proteobacteria* and *Bacteroidetes* phyla, with sequence matches to members of the *Desulfovibrionaceae*, *Flammeovirgaceae*, *Rhodobacteracerae*, *Sphingobacteriaceae*, and non-identified Coral Black Band Disease isolates. Although they found very little difference in the presence of OTUs between the three tissue types, most of the OTUs were far more abundant within root/rhizome tissues, suggesting this is the primary zone for any functional interactions between the plant and its endobiome (Garcias-Bonet et al. 2012).

Fungal endophytes are also prevalent within seagrass tissues, and may enter actively by physical or chemical penetration of the plant tissue (Schulz and Boyle 2006). Kuo et al. (1981) observed lysis of the external cell walls of *Posidonia australis* by fungal hyphae. Conversely, Nielsen et al. (1999b) found no evidence for vesicular-arbuscular mycorrhizae—fungi penetrating root tissues and maintaining an external component—in *Zostera marina* and *Thalassia testudinum*. More recent evidence has revealed a range of fungal endophytes inhabiting the leaves, roots and rhizomes of several species of tropical and temperate seagrasses including: *Thalassia testudinum*, *Halodule bermudensis* and *Syringodium filiforme* (Wilson 1998) *Halophila ovalis* (Devarajan et al. 2002); *Halodule wrightii* and *Thalassia testudinum* (Mata and Cebrián 2013); *Zostera marina*, *Zostera japonica* and *Phyllospadix scouleri* (Shoemaker and Wylie-Echeverria 2013); *Cymodocea serrulata*, *Cymodocea* sp., *Halodule beaudettei*, *Halodule uninervis*, *Halodule* sp., *Syringodium* sp. and *Thalassia* sp. (Venkatachalam et al. 2015); and *Enhalus acoroides* (Sakayaroj et al. 2010; Ling et al. 2015).

Due to their highly intimate spatial association with the plant, it might be expected that enophytic microbes have the largest influence on seagrass health and physiology, but we currently know the least about the activities and functional roles of these microbes. It is likley that they include mutualistic partners, in addition to parasites and pathogens. Given the important role that endophytic microbes play in terrestrial plant physiology (Rosenblueth and Martinez-Romero 2006), it follows that an important step for developing our understanding of seagrass microbiology is a characterisation of the function, rather than simply the composition, of endophytic microbial assemblages.

### 12.3.3 The Sediment

Shallow water marine sediments are characterised by steep chemical gradients, which are shaped by the activity of the microbes that live between sediment grains and utilise the diverse suite of electron donors and acceptors available to them. The water-logged state of sediments means solute transport primarily takes place via molecular diffusion, which over distances of more than a few millimetres to centimetres is an extremely slow process, and the spatial distribution of substrates for metabolic processes in the sediment are therefore largely controlled by their rate of consumption by microorganisms. As a result of their effect on microbial growth rates, biogeochemical processes in the sediment are distributed according to their energetic yield, with the more energetically advantageous processes found near the sediment surface and less energetically favourable process taking place in the layers below (Canfield 1993). As oxygen is the most energy yielding electron acceptor, it is rapidly consumed in the upper most sediment layers where heterotrophic organisms degrade organic carbon through aerobic respiration (Revsbech et al. 1980). Marine sediments are therefore generally divided into two major compartments; namely the oxic surface sediment and the deeper (mm—cm below the surface), reduced anoxic sediment.

The particle size of seagrass sediments varies depending on the geological and hydrological nature of the region, and can range from coarse calcareous sediments, such as those that are often found in the Great Barrier Reef, Australia, to medium and fine sandy sediments, often found in catchments and near shore environments.

The seagrasses themselves affect sediment particle composition by trapping fine particles from the water column, resulting in increased sedimentation rates (Madsen et al. 2001; Hendriks et al. 2008). Sediment particle size directly influences the transport of oxygen into the sediment through the resulting pore-size distribution, where more coarse sediment tends to experience more convective flow and less resistance to diffusion, whereas fine sediments have little convective flow and high diffusive resistance (Huettel and Webster 2001). Finer sediments therefore tend to be anoxic closer to the surface and are characterised by steeper chemical gradients compared to the more porous sediments.

As a result of intensive organic loading, seagrass sediments often have a high content of organic matter (OM) (Kennedy et al. 2010; Lavery et al. 2013) originating from both particulate organic carbon (POC), consisting mainly of seagrass detritus (leaves, root and rhizome) along with organic particles trapped from the water column (Hendriks et al. 2008), and dissolved organic carbon exuded from the seagrass rhizome and roots (Moriarty et al. 1986a, b; Long et al. 2008). Seagrass detritus, and thereby the sediment, contains significant amounts of structural, polymeric molecules such as cellulose, hemicelluloses and lignin, which are relatively resistant to microbial degradation and forms the basis for long term accumulation of organic carbon in the anoxic sediments; recently termed "Blue Carbon" (see Sect. 4.1) (Moriarty et al. 1986b; Ziegler and Benner 1999; Macreadie et al. 2014a).

### *12.3.4 The Rhizosphere Microenvironment*

Seagrasses use rhizomes and roots to anchor themselves to the sediment, with the number of rhizomes per square meter of seagrass meadow often reaching into the thousands (Brown and McLachlan 2010). The rhizomes are typically buried in the top few centimetres of the sediment and form a densely woven mat of organic material intercalated by sediment grains, with roots extending in bundles from the rhizomes and into the anoxic environment below. The combined surface area of roots in seagrass meadows ranges between 0.89 and 1.4 $cm^2$ $cm^{-3}$ depending on the seagrass species (Smith et al. 1979; Duarte et al. 1998), highlighting the potential for interaction between the seagrass and the microbes within the immediately adjacent sediment, in what is known as the rhizosphere.

The rhizosphere is characterized by the region of sediment where concentrations of plant exudates are high. It includes the rhizome as well as the roots, and represents an extremely dynamic and complex environment, which is modulated both spatially and temporally through the activity of the plants (see also Chap. 18). Seagrass roots directly influence sediment microbial activity and composition (Moriarty et al. 1985; Pollard and Moriarty 1991; Jensen et al. 2007) through the release of DOC, the amount of which may represent up to 10% of the net primary production of the plant (Moriarty et al. 1986b; Ziegler and Benner 1999) and which constitutes a mix of both large (>10.000 daltons) and small, easily degradable organic molecules such as organic acids (Wetzel and Penhale 1979; Long et al. 2008). In addition to being enriched in exuded organic molecules, the rhizosphere often also includes a microzone of elevated oxygen levels, reaching up to a few hundred micrometres away from the tissue surface (Pedersen et al. 1998; Jensen et al. 2005; Brodersen et al. 2015). In order to support plant tissue respiration in anoxic sediments, oxygen is transported from the shoots into the below ground biomass via gas phase diffusion (Greve et al. 2003). Here, excess oxygen is leaked into the sediments along with DOC (Wetzel and Penhale 1979), creating a redox gradient from the tissue surface and into the surrounding sediment, thereby greatly expanding the total volume of oxic sediment beyond the sediment surface (e.g. Pedersen et al. 1998; Jensen et al. 2005). The resulting chemical zonation formed in the rhizosphere provides an important and dynamic environment for a diverse group of microorganisms (Fig. 12.2), and metabolic rates are generally high in these regions compared to the surrounding sediment (Blackburn et al. 1994).

The spatial extent, or diameter, of the rhizosphere depends on the level of activity of the plant as well as that of the surrounding microbes, and is therefore affected by the day-night light cycle. A daytime increase in the microbial productivity of the seagrass rhizosphere has been observed previously, which was suggested to occur as a consequence of an increase in the exudation of DOC

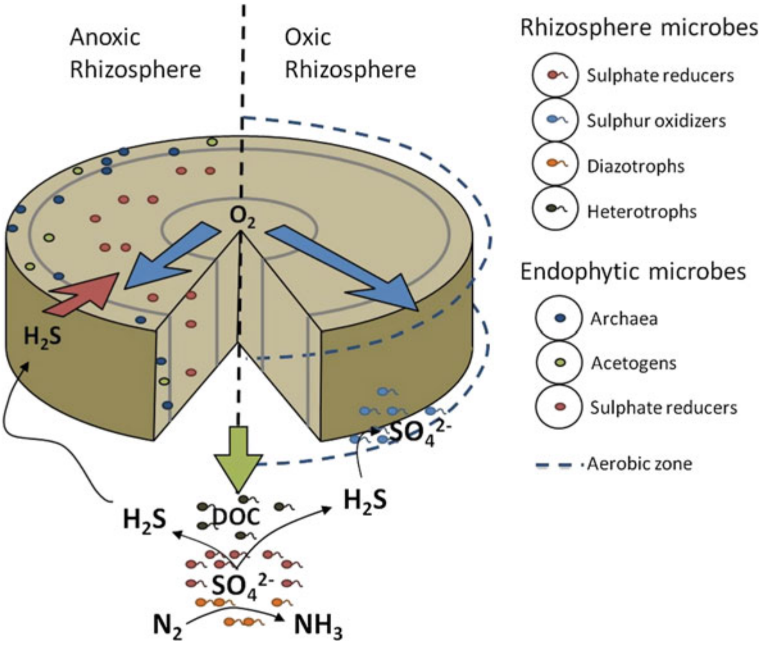


**Fig. 12.2** Schematic diagram of the cross section of a seagrass root. The extent of oxygen transport out of the root, along with the release of dissolved organic carbon (DOC) dictates microbial processes in the rhizosphere as well as among endophytic assemblages inside the seagrass tissue

resulting from photosynthetic activity of the seagrass in the light (Moriarty and Pollard 1982; Moriarty et al. 1986b). Similarly, the release of oxygen into the rhizosphere has been shown to depend strongly on the photosynthetic activity of the plants, where changes in the oxygen partial pressure within the plant over the day-night cycle dictates the expansion or retraction of the oxidised zone around the rhizome and root tissue.

By modifying rhizosphere chemistry both directly through excretion of organic compounds and indirectly by interacting with the rhizosphere microbiology, seagrasses engineer their environment to suit their needs. This results in a change in the zonation of geochemical processes in the sediment, which become arranged relative to the chemical gradients from the tissue surface as opposed to the sediment surface itself. Here, aerobic processes such as sulphide oxidation may take place in the otherwise anoxic subsurface sediment close to the oxidised tissue, whereas strictly anaerobic processes, including sulphate reduction, are limited to the region outside of this transiently oxic zone.

## 12.4 Roles of Microbes in Seagrass Systems

Arguably the most important influence of microbes within seagrass habitats is the role they play in chemical cycling processes. Microbial activities fundamentally control biogeochemical cycling in seagrass meadows (Fig. 12.1), and in the following sections we will discuss the chemical transformations and processes that underpin the carbon, nitrogen and sulfur cycles within seagrass meadows. Following this, we will discuss the effects of microbial pathogens on seagrass ecosystems.

### *12.4.1 Carbon Cycling*

Bacteria use carbon within seagrass sediments for energy (acquired through catabolic or dissimilatory metabolism) and access to material from the environment that can be used for cell synthesis (through anabolic or assimilatory metabolism), and in turn act as the major mediators of carbon cycling within seagrass habitats. In this section, we will: (1) provide a broad overview of microbial cycling of carbon within seagrass meadows; (2) discuss the varying roles of bacteria in the cycling of leaf and rhizosphere carbon; (3) explore how microbes affect decomposition of seagrass carbon; (4) describe how environmental conditions affect the microbial remineralization of carbon; and (5) illustrate the importance of seagrass meadows in biogeochemical cycling of carbon at large scales (i.e. carbon sequestration capacity).

Bacteria access carbon from several sources within a seagrass meadow, with the main pools being: (1) carbon bound within the plant material itself, which varies among species, but can generally be divided into leaf, root, and rhizome components; (2) root exudate carbon that is released into the rhizosphere during photosynthesis; and (3) externally-produced ‘allochthonous’ carbon (e.g. terrestrial and sestonic carbon) that is trapped and stored by seagrasses (Macreadie et al. 2014a). In addition, bacteria inhabiting seagrass sediments also comprise a significant fraction of sediment carbon themselves (Danovaro and Fabiano 1995). The extent to which bacteria recycle their own carbon (e.g. in the form of microbial necromass) is not well known, and therefore will not be discussed in this section, although it remains an interesting avenue for future research.

The rhizosphere is an important region for carbon cycling since it provides consistent sources of labile C for bacteria, while the seagrass is still living (Moriarty et al. 1986a). A relatively large proportion of photosynthetic carbon production (5–17%) can be released as plant exudates (Moriarty et al. 1986a; Holmer et al. 2001), and as a consequence it has been estimated that bacteria in seagrass sediments acquire 40–60% of their carbon requirements directly from DOC exuded from the rhizome and roots, with the remainder provided by seagrass detritus (POC) (Kaldy et al. 2006). Exudates released into the rhizosphere are highly labile and quickly consumed (Moriarty et al. 1986a), but it has been suggested that incorporation of this carbon into microbial biomass transfers this carbon to a more refractory pool (Kaldy et al. 2006). The composition of rhizosphere-colonising microbes is dependent on the nature of carbon resources and oxygen availability (Jensen et al. 2007). For example, oxidised regions of the root host aerobic taxa, while non-oxidised regions primarily host sulphate reducing bacteria (Jensen et al. 2007). Until recently, it was thought that fungal endophytes did not exist in association with seagrass rhizomes or roots (Nielsen et al. 1999), but recent evidence for the presence of seagrass mycobionts associated with the rhizome/roots in both temperate (Shoemaker and Wyllie-Echeverria 2013; Torta et al. 2015; Vohník et al. 2015) and tropical (Venkatachalam et al. 2015) seagrass species suggests that fungi may also play a role in the assimilation of carbon exuded from healthy plants.

The degradation of seagrass detritus, in the form of POC, is among the most important components of carbon cycling within seagrass meadows. Indeed, it is estimated that microbes break-down most leaf biomass in the first few weeks of decomposition, with the majority ($\sim 80\%$) of remineralised leaf carbon being respired to $CO_2$ (Blum and Mills 1991) and nearly all of the C remineralised within the first year of decomposition (Cebrián et al. 1997). Seagrass below-ground biomass, which in some species can create dense ‘mattes’ of rhizome, roots and sheaths, typically takes longer to decompose due to higher inherent recalcitrance of the plant material and the predominantly anoxic conditions within the sediments (Mateo et al. 2006).

The first stage of microbial utilisation of seagrass carbon after senescence or death is the passive leaching of soluble carbon, which is generally highly labile (e.g., sugars, amino acids, phenolics) and thus rapidly consumed by bacteria (Zieman et al. 1984; Vichkovitten and Holmer 2004; Maie et al. 2006). This leaching phase typically lasts 3–14 days and supports increases in microbial *r*-strategists, including members of the $\alpha$- and $\gamma$-*Proteobacteria*, due to their ability to rapidly colonize and utilise labile compounds (Josselyn et al. 1986; Peduzzi and Herndl 1991; Neubauer et al. 2004; Vichkovitten and Holmer 2004).

Once leaching is complete, bacteria and/or fungi begin to breakdown seagrass derived POC using extracellular enzymes, such as α-amylase (starch), β-D-glucosidase, β-D-galactosidase (holocellulose) and laccase and peroxidases (lignin, aromatics) (Cuomo et al. 1987; Raghukumar et al. 1999; Bongiorni et al. 2005; Panno et al. 2013). The rate of POC breakdown is much slower than the leaching phase and depends on several factors, including oxygen availability (sediment surface vs. buried), carbon quality (i.e. the nutritional value or 'lability' of the carbon), and access to other nutrients and electron donors/acceptors required to fuel microbial metabolism. Ultimately, the rate of breakdown of POC within sediments is dictated by the sediment redox chemistry, which determines the composition of the microbial communities and the dominant respiration processes at different sediment depths. During the active decomposition phase, the bacterial community shifts to one dominated by *K*-strategists that often have the capacity to degrade more recalcitrant compounds (Wahbeh and Mahasneh 1985; Trevathan-Tackett et al. unpublished). For instance, the relative abundances of Actinomycetes, *Cytophagia* and *Arthrobacter* have been shown to increase during later stages of seagrass decay, which has been linked to the degradation of celluloses, starch and aromatic compounds (Wahbeh and Mahasneh 1985; Rosselló-Mora et al. 1999; Trevathan-Tackett et al. unpublished). Fungal and protist saprophytes also play important roles in the remineralisation of more refractory materials, including polysaccharides and lignocelluloses (Cuomo et al. 1987; Raghukumar et al. 1999; Bongiorni et al. 2005; Panno et al. 2013). The ability of eukaryotic microbes to aerobically breakdown large molecules highlights their role and importance in carbon cycling by providing other heterotrophs with a source of low-molecular weight carbon (co-metabolism; Bongiorni et al. 2005; Panno et al. 2013).

Recent recognition of the importance of long-term carbon accumulation within seagrass ecosystems has drawn attention to their ability to act as important carbon sinks (McLeod et al. 2011; Fourqurean et al. 2012; Macreadie et al. 2014a), which is discussed in detail elsewhere in this book and therefore will not be covered in detail here. We will, however, briefly discuss the role of microbes in the process of carbon sequestration by seagrass meadows.

Microbes are considered the 'gatekeepers' of the global carbon cycle because they dictate how much carbon becomes sequestered versus how much is respired as $CO_2$ and returned to the atmosphere (Arnosti 2011). Defining the biotic and abiotic processes that determine the efficiency of bacterial degradation of carbon within seagrass meadows is therefore fundamental to understanding the factors that underpin carbon sequestration by seagrass ecosystems. Shifts in the metabolic activity and composition of bacterial assemblages, changes in sediment chemistry and variability in the lability of carbon will all influence the microbial processes that ultimately influence carbon burial. As a consequence of the balance of these processes, the carbon in seagrass sediments essentially has three fates: (1) carbon (either in the form of POC or DOC) that is recalcitrant to microbial degradation remains stored within the sediment for prolonged periods, while labile carbon is recycled by heterotrophic bacteria and is either (2) assimilated into microbial biomass or (3) respired as $CO_2$.

For the most part, sequestered carbon is organic carbon that has made its way into deep sediments, where anoxic conditions support long-term preservation. Microbial metabolism within anoxic sediments is dominated by the sulphate reducing bacteria, although their abundances and activity typically decreases with depth (Marba et al. 2006), with shifts towards dominance by methanogenic Archaea as sulfate availability decreases. Additionally, other conditions or processes can promote organic carbon preservation in sediments such as geopolymerisation to form humic substances, physical protection of labile compounds by refractory compounds or minerals and the selective preservation of inherently refractory compounds (reviewed in Burdige 2007). It is important to note, however, that 'preserved' carbon buried within deep sediments is still susceptible to disturbance (Macreadie et al. 2015). For example, bioturbators (e.g. crabs, shrimp, worms) can alter sediment chemistry and microbial processes by increasing the flow of oxygen into sediments, consequently exposing preserved carbon to microbial attack (Atwood et al. 2015).

In summary, microbes are primary drivers of carbon cycling in seagrass ecosystems. They play an important role in processing carbon in healthy plants (e.g. rhizosphere microbes) and in decaying plants (e.g. leaf and sediment microbes). They have the ability to process carbon produced by the plants themselves (autochthonous carbon), as well as externally-produced carbon (allochthonous carbon) that is captured by sequestered by seagrasses. Microbial processing of carbon within seagrass ecosystems is influenced by a variety of biotic (e.g. bioturbation) and abiotic (e.g. intrinsic recalcitrance of carbon molecules) factors. Given the fundamental role of microbes in controlling carbon sequestration by seagrasses ecosystems, there is good reason to understand their carbon-cycling roles in more detail, particularly through process-based studies aimed at further teasing apart the specific bacterial, fungal and protistan taxa and their functions within seagrass meadows under varying environmental conditions in order to better understand optimal conditions for carbon sequestration.

### *12.4.2 Nitrogen Cycling*

Seagrasses have a high nutrient demand, and their productivity is often limited by the availability of nitrogen (Touchette and Burkholder 2000). The successful growth and high productivity of seagrasses in oligotrophic waters is probably due to their ability to take up nutrients through both leaves and roots (Hemminga 1998), allowing them to outcompete other organisms for nutrient uptake (Duarte et al. 2005). There is evidence that different parts of the plant may preferentially take up different forms of nitrogen, with uptake rates for the tropical species *Thalassia hemprichii*, *Halodule uninervis* and *Cymodocea rotundata* being greatest for $NH_4^+$,

$NO_3^-$ and urea in leaf tissues, and for $NH_4^+$ and amino acids in roots (Vonk et al. 2008). Concentrations of $NH_4^+$ and amino acids in sediment porewaters are directly related to the microbial remineralisation of organic matter, and are therefore highly temporally dynamic in coastal sediments (Canfield et al. 2005). The high affinity of seagrass roots for both dissolved inorganic nitrogen (DIN) and dissolved organic nitrogen (DON) species enables the fast uptake of N from freshly deposited organic matter (Evrard et al. 2005; Barrón et al. 2006), and thus may allow seagrasses to out-compete sediment microorganisms for N (Vonk et al. 2008). Indeed, the ability of the plant to out-compete bacteria for $NH_4^+$ could explain the low rates of microbial nitrification observed in some seagrass meadows (Risgaard-Petersen et al. 1998; Ottosen et al. 1999; Welsh et al. 2000). However, in many seagrass meadows the porewater nutrient concentrations may be insufficient to support the plants' high N demand (Welsh 2000). In these cases, plant-specific interactions with diazotrophic—or N fixing—bacteria, which are able to grow using molecular nitrogen ($N_2$) in the absence of an alternative nitrogen supply, are therefore key to the productivity and resilience of seagrasses on the meadow scale (Welsh 2000).

An important concept within the holobiont paradigm is that of the host plant and its microbiome as an "integrated functional unit" (Ofek-Lalzar et al. 2014). By far the best example of this idea for seagrasses is their relationship with diazotrophs in the rhizosphere, where nitrogen fixing microbes are 50- to 300-fold more abundant, relative to bulk sediments (Patriquin and Knowles 1972). Nielsen et al. (2001) found that within rhizosphere sediments of *Zostera noltii*, up to 31% of N fixation could be attributed to bacteria directly inhabiting the roots and rhizomes. However, this relationship is probably both seagrass species-specific and latitude-dependent. For example, N fixation rates in temperate seagrasses can account for 5–25% of the plant's N requirements, whereas this figure may reach greater than 65% for tropical species (Welsh 2000; Devereaux 2005).

Nitrogen fixation activity has been measured primarily using whole-plant sediment cores or rhizosphere sediment slurries, and then scaled to the meadow level using estimates of mg N fixed $m^{-2}$ $day^{-1}$. It is often difficult to assess the degree of comparability between different methodologies (Welsh 2000). However, it is clear that the range of values reported for N fixation rates in seagrass meadows (0.03–140 mg N $m^{-2}$ $day^{-1}$) is greater than that reported for unvegetated sediments (0.07–0.54 mg N $m^{-2}$ $day^{-1}$), depending on the location and seagrass species (Welsh 2000, and references therein). The unique nature of the seagrass microbiome is highlighted by the fact that the majority of N fixers in marine sediments and seagrass meadows belong to taxa of sulphate reducing bacteria such as *Desulfovibrio* (Blaabjerg and Finster 1998; Blaabjerg et al. 1998). Accordingly, rates of both N fixation and sulphate reduction are elevated in the rhizospheres of many different species of seagrass, and their depth distribution tends to follow seasonal changes in root biomass (Welsh 2000). On the meadow scale, 25–95% of N fixation may be attributed to sediment/rhizosphere sulphate reducing bacteria (Capone 1982; Welsh et al. 1996; McGlathery et al. 1998).

Sulphate reducing bacteria are carbon limited, and N fixation by sulphate reducing bacteria therefore follows diurnal patterns related to the plant's exudation of photosynthetic products (DOC) through the roots (O'Donohue et al. 1991; Blackburn et al. 1994; Welsh et al. 1997; Blaabjerg et al. 1998; Hansen et al. 2000; Holmer et al. 2001; Nielsen et al. 2001; Holmer and Laursen 2002). Since the availability of labile carbon may be the primary factor limiting N fixation rates in marine sediments (Welsh 2000), this is an example of how the plant is potentially able to regulate its associated microbiome to increase N supply.

In addition to sediment and rhizome associated bacteria, endophytic bacteria also link both N fixation and sulphate reduction in seagrass systems. Sulphate reducing bacteria isolated from *Z. marina* roots (e.g. *Desulfovibrio zosterae*) are capable of N fixation (Nielsen et al. 1999). Additionally, among the bacterial endophytes of *Posidonia oceanica*, Garcias-Bonet et al. (2012) identified genes involved in N fixation (*nifH*), suggesting that the internal seagrass microbiome has a similar role in the plant's nutrient provision to that of the more well-studied rhizosphere community. Indeed, Devereaux (2005) visualised the seagrass root cross-section as a redox gradient to some extent mirroring that of the rhizoplane, wherein bacterial endophytes withstand the exudation of oxygen from plant roots during the day, and are able to metabolise their preferred electron acceptors as the oxygen gradient recedes into deeper cortex layers during the night. Since the activities of the various microbial nitrogen cycling consortia are tightly controlled by $O_2$ availability, this raises the intriguing possibility that the plant is also able to mediate internal biogeochemical functions via photosynthesis.

Less is known of the role of leaf epiphytes in the provision of, or competition for, nitrogen. Crump and Koch (2008) showed that *Zostera marina* leaves host a bacterial community primarily composed of Bacteroidetes and α-*Proteobacteria*, but a relatively low abundance of diazotrophs. While significant levels of nitrogenase activity have been attributed to epiphytic cyanobacteria (e.g. Goering and Parker 1972; Pereg et al. 1994; Hamisi et al. 2004), several studies have indicated that phyllosphere communities do not make a significant contribution to overall N fixation (Capone 1982; O'Donohue et al. 1991; Welsh 2000).

Given that seagrass leaves appear to preferentially take up inorganic, rather than organic, nitrogen species (Vonk et al. 2008), the possibility of a functional relationship between the plant and nitrifying microbes is intriguing. However, whether these epiphytic nitrifiers contribute to or compete with plant DIN uptake is yet to be shown. Denitrifying bacteria, whose activity is often coupled to the nitrification process, have been found in greater abundances within *Thalassia hemprichii* and *Halodule uninervis* rhizosphere sediments ($10^3$–$10^4$ cells g wet wt$^{-1}$), compared to non-rhizosphere sediment ($\leq 10^3$ cells g wet wt$^{-1}$), with these elevated levels of denitrifying bacteria accompanied by detectable rates of denitrification activity, which increased in the presence of both glucose and $NO_3^-$ (Shieh and Yang 1997). The supply of $NO_3^-$ and organic substrate are the primary factors regulating denitrification activity in coastal sediments (Herbert 1999), whereas nitrification rates are dependent on $NH_4^+$ concentrations and $O_2$ availability (Rysgaard et al. 1995). However, measured rates of denitrification and coupled nitrification-denitrification are often low in seagrass meadows compared to unvegetated sediments (ranging from 0.4 to 150 μmol N m$^{-2}$ h$^{-1}$ compared to 50–250 μmol N m$^{-2}$ h$^{-1}$; Marbà et al. 2006, and references therein). This may be attributed either to competition for ammonium between the plant and nitrifying bacteria, which supply the $NO_3^-$, or to direct competition for $NO_3^-$ under eutrophic conditions (Risgaard-Petersen and Ottosen 2000; Welsh et al. 2001; Romero et al. 2006). Blackburn et al. (1994) showed that denitrification rates in a *Halodule beaudetti* meadow were higher at night, when both plant $NO_3^-$ uptake and $O_2$ release were lower. Alternatively, it has also been suggested that denitrification may be more important in association with seagrasses that release greater amounts of oxygen from their roots, thereby supporting coupled nitrification-denitrification (Hemminga and Duarte 2000; Romero et al. 2006; McGlathery et al. 2007). However, seasonal variations observed in meadows underlying eutrophic waters, indicate that denitrification rates are tied to $NO_3^-$ concentrations in the overlying water rather than coupled with nitrification (Risgaard-Petersen and Ottosen 2000). Further investigation into the specific interactions between seagrass and nitrifying and denitrifying microorganisms should provide more information on the specific functional role of these microbial communities in maintaining the health and productivity of seagrass meadows.

In summary, seagrasses host specific N-cycling consortia, which: (1) fulfill important functional roles at both the plant and meadow scale; and (2) link the major elemental cycles in seagrass meadows via the dual metabolic capability of diazotrophic, sulphate reducing bacteria, which additionally contribute to the consumption of DOC in the root-rhizome. There is a great deal of evidence that N fixers are key components of both the internal and external seagrass microbiome, as well as the wider sediment environment; and thus contribute to meadow-scale nitrogen provision. However, there is no clear consensus on the importance of either nitrifying and denitrifying microorganisms in seagrass systems. An increased use of molecular tools to target specific microbial groups, combined with biogeochemical rate measurements, should be a focus of future research efforts to elucidate N cycling in seagrass meadows.

### *12.4.3 Sulphur Cycling*

Within anoxic marine sediments, sulphate ($SO_4^{2-}$) is the major electron acceptor available for microbial respiration (Jørgensen 1982), with concentrations of sulphate often orders of magnitude higher (mM versus µM concentrations) than other potential electron acceptors and rarely limiting. Dissimilatory sulphate reduction (SR) is an anaerobic process carried out by heterotrophic bacteria and archaea in anoxic sediments, where sulphate is reduced to elemental sulphur ($S^0$) or hydrogen sulphide ($H_2S$) via the oxidation of organic carbon (Fenchel et al. 2012). While this process yields significantly less energy per unit compared to oxygenic respiration, sulphate reducing organisms are ubiquitous in anoxic habitats, and owing to the large volume of anoxic sediment in coastal marine ecosystems, approximately half of the organic carbon in the sediment is oxidised through SR (Jørgensen 1982; Canfield 1989). Due to the high levels of carbon input to seagrass sediments, SR rates are typically significantly higher in seagrass meadows compared to non-vegetated sediments (Isaksen and Finster 1996; Holmer and Nielsen 1997; Holmer et al. 2001, 2003).

The close link between the seagrass and the rhizosphere microbial community is demonstrated particularly well by how SR rates in carbon limited sediments often follow the daylight cycle, with rates increasing towards the midday, when light influx to the seagrass meadow is higher (Moriarty et al. 1986b; Pollard and Moriarty 1991; Welsh et al. 1996; Blaabjerg et al. 1998). As the light increases, so does the photosynthetic activity of the seagrasses, resulting in a higher carbon fixation rate and increased exudation of DOC to the sediment, which consequently supports elevated microbial activity.

The stimulation of SR by seagrasses seems somewhat counter-productive from the plants' perspective, as SR results in the formation of the phytotoxin hydrogen sulphide (Lamers et al. 2013), which is believed to play a major role in seagrass die-off events (Carlson et al. 1994; Greve et al. 2003; Borum et al. 2005; Calleja et al. 2007). However, as described above, sulphate reducing bacteria have been shown to account for a significant proportion of the nitrogen fixation in these sediments, with rates often exceeding that of non-seagrass sediments by several orders of magnitude (Welsh et al. 1996; Donnelly and Herbert 1998; Nielsen et al. 2001). So while on one hand the increased SR may negatively impact the seagrass through toxic sulphide production, the increased fixation of nitrogen as well as overall turnover of organic material likely imposes major benefits during nutrient limited conditions, as is often the case in tropical marine ecosystems. However, a negative relationship between the below ground biomass density and SR has also been observed in meadows of *Posidonia oceanica* (Holmer et al. 2003), suggesting that the interaction between seagrasses, their microbiota and sediment biogeochemistry vary among species, with interactions likely governed by the growth strategy of the seagrass and the level to which it excretes DOC (Wetzel and Penhale 1979), sediment oxygen levels, or both, in addition to the availability of carbon from alternative sources (Boschker et al. 2000).

The continuous diffusion of oxygen from seagrass roots and rhizomes profoundly affects the microbial processes in the rhizosphere. In healthy seagrass meadows, the sediment pool of hydrogen sulphide is often lowered during day time (Blackburn et al. 1994, Carlson et al. 1994; Lee and Dunton 2000; Holmer et al. 2001; Borum et al. 2005), primarily as a result of oxygen being released into the sediment by the seagrass, which enables chemical re-oxidation of the sulphide even in deep sediments (Brodersen et al. 2015). However, the release of oxygen into the sediment may also support the activity of sulphide oxidizing bacteria at the oxic-anoxic interface close to the tissue surface. In a recent study of the salt marsh cord grass S*partina alterniflora,* gene transcripts associated with sulphide oxidizers were primarily detected in the upper 5 cm of the sediment where the root density was highest, and transcription of specific sulphide oxidizing genes tended to be higher on the root surface compared to the surrounding sediment (Thomas et al. 2014). The release of oxygen from roots and rhizomes is proposed to protect plants that live in reduced sediments from sulphide poisoning (Blackburn et al. 1994;

Pedersen et al. 1998; Borum et al. 2005; Brodersen et al. 2015), and a reduction in the oxidation of the immediate rhizosphere during conditions of lowered photosynthetic activity or reduced water column oxygen concentration is considered to be an important step in seagrass die-off cascades (for further details see Chap. 18).

Oxidation of sulphide in seagrass meadows may also take place through the activity of other organisms. Bioturbators are known for oxidising the sediment through their burrowing activity, resulting in mixing of oxidised water into the anoxic sediment, or directly through pumping of water into their burrows (bio-irrigation) to support their own respiration (Kristensen et al. 2012). In a recent study, sediment dwelling lucinid bivalves were proposed to be of importance to seagrass meadows especially in sub-tropical and tropical waters (van der Heide et al. 2012). These bivalves, which may reach densities of 10–1000 s per square meter, live in symbiosis with sulphide oxidizing bacteria residing in their gills (Cavanaugh 1983), and have been hypothesised to form a tripartite symbiosis with the seagrasses in which the bivalve benefits from the high sulphide production in the sediments, while the seagrass benefits from sulphide removal performed by the bacteria living within the bivalves. Indeed, the presence of lucinid bivalves in sediment amended with sulphide increased the shoot biomass of *Zostera noltii* by 1.9 fold (van der Heide et al. 2012).

A recently discovered filamentous bacteria belonging to the *Desulfobulbaceae* has been shown to oxidise sulphide up to several centimetres into anoxic sediment via direct transportation of electrons to the oxic surface (Nielsen et al. 2010; Pfeffer et al. 2012). While their general ecological importance is still unknown, it is tempting to suggest that such organisms could also play a role in removal of sulphide in the stabilised sediment of seagrass meadows. However, this remains to be investigated.

### *12.4.4 Pathogens*

Marine organisms, particularly sessile benthic organisms such as coral and macrophytes, are constantly in contact with high concentrations of microorganisms, including a broad array of potentially harmful pathogens and parasites (Engel et al. 2002). As a consequence many marine animals and plants produce secondary metabolites used to defend themselves against microbial attack (Pawlik 1993; Engel et al. 2002; Lane and Kubanek 2008). However, in recent years, there has been an increase in the incidence of marine disease outbreaks, which have been linked to changes in climate, host stress and increased transport via human activities such as pollution or international shipping (Harvell et al. 1999).

Very few microorganisms have been reported to have deleterious effects on seagrasses. A protozoan parasite Plasmodiophora was reported to infect *Halodule wrightii* in the Gulf of Mexico (Walker and Campbell 2009) and was subsequently isolated from seagrasses in Florida and the Caribbean (Neuhauser et al. 2011). However, this parasite has never been recorded in Australia, and the overall transmissible characteristics seem to be limited. The more devastating and well-known seagrass pathogen is the stramenopile protist *Labyrinthula*, which has been identified as the causative agent of wasting disease (reviewed in Sullivan et al. 2013). Ecologically, *Labyrinthula* primarily functions as a globally prevalent saprobe of detritus (Leander and Porter 2001), and thus is important for nutrient cycling in seagrass meadows. However, it has been hypothesized that *Labyrinthula* can act as an opportunistic pathogen (Muehlstein et al. 1991). While some seagrasses have been shown to be able to produce anti-labyrinthulid defenses (Brakel et al. 2014; Trevathan-Tackett et al. 2015), it is hypothesised that seagrasses become susceptible to disease when they are immunologically compromised from one or more environmental stressors including temperature, salinity and shading (Koch et al. 2007a, b). The details of the mode of infection are still unclear, but the result is consistent, whereby a distinct area of necrosis or black/brown lesions is formed surrounded by healthy, green tissue (Fig. 12.3). Once the lesion(s) spread the width of the blade, resource transport is blocked, and the leaf dies soon after. Localized spreading of infection occurs with leaf-to-leaf contact, but large-scale dispersal can be promoted by exported detritus.

*Labyrinthula* has been implicated as the causative agent of infrequent but devastating large-scale seagrass die-offs. For instance, 90% of *Zostera marina* habitats

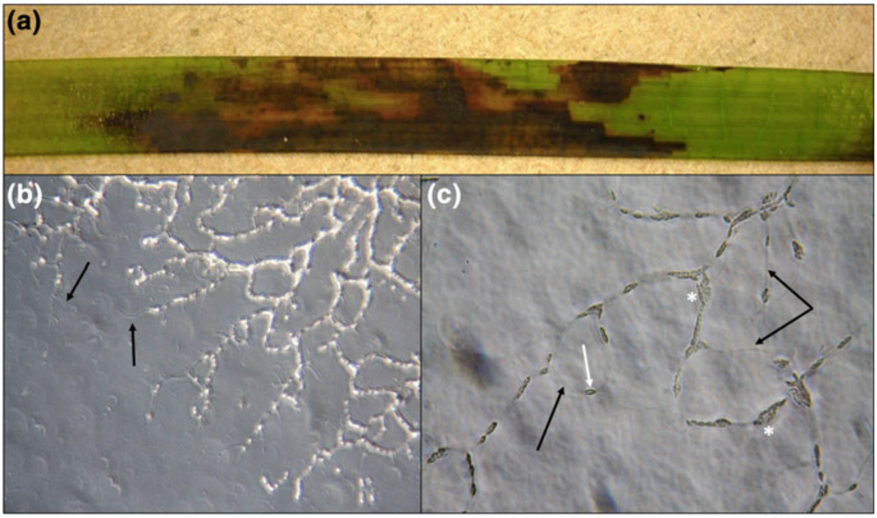


**Fig. 12.3** Seagrass wasting disease and the opportunistic pathogen *Labyrinthula.* **a** An example of a green seagrass leaf exhibiting a lesion, symptomatic of wasting disease cause by pathogenic *Labyrinthula*. Lesions may begin patchy, but can become extensive, eventually bisecting the leaf and blocking resource transport. **b** and **c** *Labyrinthula* isolated from a seagrass in Victoria, Australia growing on agar media. *Labyrinthula* is a single-celled (white arrows) but colonial (clumping at white asterisks) protist that is a ubiquitous saprobe of marine plant detritus. It attaches and moves within an ectoplasmic network (black arrows) of actin/myosin. *Photo credits* S.Trevathan-Tackett

were affected in the 1930s along the coasts of the USA and Europe, with, for instance, 40 km$^2$ of *Thalassia testudinum* habitat lost in Florida Bay (USA) during the 1980s (Robblee et al. 1991). Other incidences of disease have been reported over the last century (reviewed in Sullivan et al. 2013), but only two cases of *Labyrinthula* outbreaks have been recorded in *Zostera* sp. meadows in Australia and New Zealand (Armiger 1964; Sullivan et al. 2013). Although reports of wasting disease are rare in Australia, *Labyrinthula* has been isolated from lesions on *Zostera mucronata* and *Z. tasmanica* and healthy *Halophila ovalis* leaves in Western Australia (Vergeer and den Hartog 1994). Given the lack of data on wasting disease in the Southern Hemisphere, there are currently efforts to elucidate the distribution, prevalence and pathogenicity of *Labyrinthula* in Australian seagrass meadows (Sullivan et al. unpublished data). Identifying the prevalence and pathogenicity of *Labyrinthula* in Australian seagrass meadows in the near future will provide a baseline for the occurrence of this ecologically relevant endophyte, which will be critical for identifying future shifts in the population and occurrence of wasting disease related to changes in climate (Harvell et al. 2002; Hoegh-Guldberg and Bruno 2010).

### 12.4.5 Microbial Influence on Seagrass Seed and Plant Growth

The role of microorganisms in seed growth and subsequent plant development is an understudied area of research. Moffler and Durako (1984) observed that axenic seedlings of *Thalassia testudinum* exhibited no growth enhancement when incubated in media amended with either organic or inorganic nitrogen; they concluded that microbial associations with this species of seagrass could play a critical role in its nutrient uptake and growth. Statton et al. (2013) showed that the addition of refractory organic matter (seagrass detritus) stimulated *Posidonia australis* seedling growth, and suggested that this was the result of microbially mediated nutrient provision. However, other studies have indicated that the addition of labile organic matter (e.g. algal detritus) can have a negative effect on seedling growth, possibly because of greater sulphide production (Terrados et al. 1999; Kilminster et al. 2006; Perez et al. 2007). In terrestrial plants, the inoculation of plants with various species of bacteria, collectively known as plant growth promoting rhizobacteria (PGPR), can increase the plant's nutrient acquisition, root growth and suppression of pathogens, sometimes in association with fungal mycorrhizae (Vessey 2003). Such specific plant-microbe interactions are yet to be shown for seagrasses.

## 12.5 Role of Microbes in Seagrass Decline and Resilience in a Changing Ocean

### *12.5.1 Eutrophication*

Changes to land use and agriculture have led to an increase in coastal nutrient loading since the pre-industrial age. This can cause eutrophication, whereby fast-growing macro- and microalgae (phytoplankton and epiphytic microalgae) rapidly increase in abundance in response to excess concentrations of N and P in the water column; often at the expense of more slow-growing plants such as seagrasses. Although eutrophication is thought to be a major contributor to the catastrophic losses of seagrass meadows observed during the last few decades (Duarte 2002; Burkholder et al. 2007), responses of seagrasses to experimentally induced eutrophication can be either positive or negative, depending upon co-varying factors such as seagrass species, mechanism of impact (e.g. increased turbidity, increased nutrient (N and/or P) load or increased shading) and effect size (i.e. "nutrient enrichment" vs. "excess nutrient loading") (Burkholder et al. 2007).

Shading caused by the overgrowth of epiphytic microalgae (in shallow areas) and phytoplankton (in deeper areas) is often assumed to be the greatest cause of seagrass decline following eutrophication (Burkholder et al. 2007; Lepoint et al. 2007). The subsequent deposition of organic material associated with increased microalgal growth onto the sea floor leads to increased oxygen consumption in the upper layers of sediment, leading to elevated production of the phytotoxin $H_2S$ due to an increased importance of sulphate reducing bacteria.

Eutrophication can occur as a result of excess N or P in the water column, although it is generally acknowledged that N is the primary cause of coastal eutrophication, globally (Howarth and Marino 2006). Interactions between seagrasses and nitrogen cycling microorganisms could therefore become more critical to plant health under eutrophic conditions. A secondary effect of increased porewater sulphides from sulphate reduction is the inhibition of the nitrification process that, coupled to denitrification, removes excess DIN from the water column (Joye and Hollibaugh 1995). In unvegetated marine sediments, rates of nitrification and denitrification may increase under eutrophic conditions as a consequence of increased substrate supply, thereby providing a mechanism for the removal of excess N from overlying waters; however, in heavily eutrophic systems ammonia oxidisers may be outcompeted for $O_2$ by heterotrophic bacteria (Meyer-Reil and Koster 2000). The significant impact of seagrasses on $O_2$ release and sediment DIN availability suggests that denitrification is probably also susceptible to changes in plant production. For example, Eyre and Ferguson (2002) showed that the efficiency of denitrification decreases as nutrient load to the water column increases, leading to DIN release to the water column, and thereby compounding the effects of eutrophication.

It is notable that the direct uptake of nutrients by seagrasses is highly variable between species and geographic regions. While it appears that under excess nutrient loading, seagrasses may shift towards an increased reliance on the supply of N and P from the water column (via leaves) rather than sediment porewaters (via roots) (Touchette and Burkholder 2000), a great deal more investigation is required into how potential environmental stressors—carbon and nutrient loading, shading, temperature and pH—impact upon seagrass physiology, growth and interactions between the plant and its microbiome.

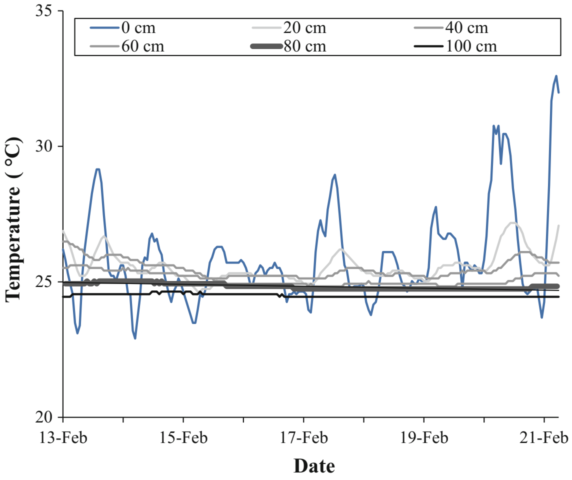
### 12.5.2 Climate Change

The IPCC predicts with a very high level of confidence that coastal systems – where seagrasses primarily occur—will be negatively impacted by three key impacts of anthropogenic climate change: increasing ocean temperatures (warming), ocean acidification, and sea level rise (IPCC 2014). Indeed, there is already mounting evidence that climate change is responsible for seagrass decline and loss of resilience (Short and Neckles 1999; Short et al. 2006; Macreadie et al. 2014b; Thomson et al. 2015; Unsworth et al. 2015). But what role do microbes play in exacerbating or ameliorating the impacts of climate change on seagrass decline and resilience? Few studies have explicitly addressed this question experimentally, but with knowledge of the important role that microbes play in biogeochemical cycling and a basic understanding of how microbes respond to changes in fundamental environmental variables (e.g. temperature, oxygen, nutrients), it is possible to make inferences about the likely responses of microbes to climate change and the concomitant impacts on seagrass decline and resilience. Here, we will focus on the likely responses of seagrass microbes to ocean warming and acidification.

Microbial activity is typically assumed to follow first-order kinetics, with elevated temperature leading to increased microbial activity (Fenchel et al. 2012). Warming of seawater has indeed been shown to increase bacterial activity in seagrass sediments (López et al. 1995; Mateo et al. 1997), and with predictions of rises in ocean temperatures of 2–4 °C during this century, it seems reasonable to expect changes in the metabolic activity of microbes within seagrass ecosystems. Predictably, surface sediments are more responsive to changes in water column temperature than deeper sediments, albeit with a slight lag, which is likely due to the time it takes for seawater to permeate into the porewater spaces of below-ground sediments. For instance, Fig. 12.4 shows changes in sediment temperatures at varying depths within a seagrass meadow in Fagans Bay, New South Wales. Thus, warming seawater temperatures are likely to have the greatest effect on aerobic heterotrophic bacteria in surface sediments.

Among aerobic heterotrophs, warming affects bacterial production (BP) and respiration (BR), which will have flow-on effects for biogeochemical processes and food webs within seagrass meadows (Brown et al. 2004; Lopez-Urrutia and Moran 2007; Pedersen et al. 2011). For example, Pedersen et al. (2011) showed that remineralisation rates for *Posidonia oceanica* belowground matte biomass in the Mediterranean Sea increased up to 4.5-times following a 10 °C increase in water

**Fig. 12.4** Variability in temperatures at different sediment depths within a seagrass meadow. Data from P. Macreadie, Fagans Bay, NSW, Australia



temperature. This is thought to be due to warming causing an increase in bacterial activity in seagrass sediments (López et al. 1995; Mateo et al. 1997), implying that carbon remineralisation may increase with warming. Other studies (e.g. Sarmento et al. 2010) have come to the conclusion that warming increases bacterial abundance and activity, thereby reinforcing the already dominant and important role of microbes in biogeochemical cycling within seagrass ecosystems. Based on these studies, we therefore predict that warming will negatively impact the ability of seagrasses to sequester carbon by increasing the activity of microbial decomposers in surface sediments.

Warming may also affect the vulnerability of seagrasses to marine diseases by influencing the growth and virulence of microbial pathogens (Burge et al. 2014). Warm-water loving microbial pathogens (e.g. Vibrio, Labyrinthula), like many other organisms inhabiting the oceans, are predicted to display poleward range expansions as sea temperatures rise (Parmesan and Yohe 2003; Baker-Austin et al. 2013; Burge et al. 2014). For example, MSX (multinucleated sphere unknown) is a disease of the commercially-important eastern oyster (*Crassotrea virginica*) that has moved poleward in the northern hemisphere with rising temperatures (Burreson et al. 2000). There is no quantitative evidence yet to show poleward migration of the seagrass wasting disease caused by Labyrinthula, but numerous studies show that the susceptibility and frequency of Labyrinthula outbreaks increases with warming seawater temperatures (Bockelmann et al. 2013). While the vast majority of studies suggest that warming will increase the vulnerability of marine organisms to pathogens, there are also some incidences of the opposite effect. For example, Olsen et al. (2015) found that climate warming alleviated pathogen (*Labyrinthula* sp.) pressure in the climate-vulnerable Mediterranean seagrass, *Posidonia oceanica*. The latter case is more likely to be a rare exception; the majority of evidence indicates that warming will increase the susceptibility and mortality of seagrasses due to microbial pathogens.

Rising levels of atmospheric $CO_2$ are reflected in oceanic surface waters, where increased $CO_2$ concentrations ($pCO_2$) lead to a reduction in seawater pH: a process termed ocean acidification (OA). OA has been shown to both negatively and positively affect microbial diversity, productivity, and function (e.g. quorum sensing, nitrogen and carbon cycling; Das and Mangwani 2015). However, current understanding of the impacts of long-term changes to ocean pH on marine microorganisms is incomplete and results so far are very mixed. For example, some studies have found that OA does not affect microbial community structure or microbially-driven biogeochemical processes (Wang et al. 2016), whereas others have found that OA destabilises the microbiomes of coastal organisms (Lesser et al. 2016). Meta-analyses performed on data collected from short-term, manipulative experiments suggests a highly variable response between different microbial functions, with processes such as carbon and nitrogen fixation increasing as a consequence of higher seawater $pCO_2$ (Joint et al. 2011; Liu et al. 2010). The effects of OA on microbes in coastal waters are further complicated by local environmental conditions. For example, Sala et al. (2016) found that microbial communities were less affected by OA in productive waters compared to oligotrophic waters.

There are no studies to date that specifically address how ocean acidification will affect microbes within seagrass meadows, although we note that the effects of ocean acidification within seagrass-dominated ecosystems may be lessened relative to impacts on unvegetated sediments, due to seagrasses having the capacity to buffer pH levels through photosynthesis. For example, several studies (Semesi et al. 2009; Hendriks et al. 2014) have shown that the intense photosynthetic activity of seagrass growing in shallow coastal lagoons can increase pH levels in the water column by ecologically-meaningful amounts (e.g. 0.5), thereby reducing potential impacts of ocean acidification on seagrass microbes, as well as lessening the impacts of climate change by sequestering $CO_2$.

Sediment microorganisms already experience fluctuating pH levels, due primarily to the production of $CO_2$ during organic matter remineralisation, coupled with other processes that affect microscale patterns in porewater pH, including nitrate and ammonium assimilation (Soetart et al. 2007). This could explain why biogeochemical processes such as nitrification, which is inhibited by reduced pH in the water column (Huesemann et al. 2002), remains unaffected by OA in sediments, where pH may also be buffered by the dissolution of carbonate minerals, when present (Kitidis et al. 2011). However, Laverock et al. (2013) showed that the impacts of OA on sediment nitrification rates were mediated by the presence of burrowing macrofauna; highlighting the importance of considering inter-species dynamics when predicting the response of an ecosystem to environmental change. This specific interaction may be particularly important in seagrass meadows, where water column nitrification could become more important for fuelling coupled nitrification-denitrification under certain scenarios of environmental change. Furthermore, the synergistic effects of different environmental stressors in the coastal zone—and the interaction between different functional groups of bacteria, some of which will be “winners” in a high-$CO_2$ world—will likely interact to produce a complex response to ocean acidification in seagrass meadows.

In conclusion, there is mounting evidence for climate change-related decline of seagrass ecosystems and loss of resilience. Here we have focused on the potential impacts of ocean warming and acidification on seagrasses, and the role that microbes might play in mediating the responses of seagrasses to these stressors. To date the availability of information in this area is very limited, which has meant we have relied heavily on the broader literature to make inferences about how the seagrasses and their microbial inhabitants might respond to climate change. Our analysis indicates that responses are likely to be mixed—i.e. positive and negative impacts of climate change on the seagrass microbiome—and will often be context dependent (e.g. responses depended on local environmental conditions such as nutrient levels or the presence of pathogens). In general, however, available evidence suggests that warming will have negative impacts on the health of seagrass meadows and their provision of ecosystem services by providing better growth conditions for microbial pathogens and decomposition of organic matter, whereas for now it is very difficult to make conclusions about the net impact (positive or negative) of OA on seagrasses via microbial pathways. Clearly there is a strong case for further research effort into understanding the impacts of climate change on the seagrass microbiome, particularly the impacts of OA.

## 12.6 Summary and Outlook

The goal of this chapter has been to convey the, often overlooked, significance of microbial processes in shaping the ecology and stability of seagrass ecosystems. Microbes play a fundamental role in maintaining the complex chemical balance required for seagrasses to flourish within often challenging coastal environments. In turn, functionally diverse populations of microorganisms benefit from the assortment of resource (i.e. growth substrates, electron donors/acceptors) rich microhabitats (e.g. leaves, rhizosphere, sediments) provided by seagrass meadows. Seagrass-microbe interactions span the continuum from symbiosis to disease and have implications that scale-up to influence ecosystem-level biogeochemical cycling.

Our understanding of seagrass-microbe interactions has been developed during the last 30 years via the application of a variety of analytical approaches, including traditional microbiological approaches used to cultivate seagrass-associated microbes (Nielsen et al. 1999; Shieh et al. 2000; Yoon et al. 2007) and biochemical rate measurements to directly measure the activities of microbes in situ (Capone 1982, 1983; Moriarty et al. 1985; Pollard and Moriarty 1991; Williams et al. 2009; Eyre et al. 2011). Mirroring progress in other areas of environmental microbiology, some the most significant recent advances have come from the application of molecular biological tools (Jensen et al. 2007). These approaches have provided a new capacity for teasing apart the diversity and functional capacity of seagrass-associated microbes and have provided a much clearer view of the ecological interactions between seagrasses and microorganisms. However, relative to other analogous microbe-host systems (e.g. corals, terrestrial plants) the application of molecular tools has only been modest, meaning that several important questions remain open. In particular, our knowledge of microbiology within the Australian seagrass ecosystems, which are the focus of this book, are especially limited. As noted in the Introduction, a lack of available information prohibited a focus in Australian systems within this chapter and we have subsequently provided a generalized description of seagrass microbiology. Efforts to characterize the composition, activity and function of microbial communities within Australian seagrass habitats is an important step towards developing a better understanding of the ecology of these important ecosystems within this region.

An important lesson that can be learnt from other fields is that molecular biological tools become most powerful when they are effectively coupled with other approaches that allow for microbial diversity to be directly linked to function and biochemistry. For instance, the coupling of molecular probes with single-cell imaging approaches such as nanoscale secondary ion mass spectrometry (NanoSIMS) provide the potential for the direct quantification of transfer of molecules of interest from specific microbes to the host and back again (Pernice et al. 2012). Other analytical chemistry approaches and metabolomic analyses also have great potential for deciphering the chemical ecology underpinning seagrass-microbe interactions. Information derived from these diverse analytical approaches can be effectively brought together using novel and ecologically powerful statistical tools, such as network analysis, which provides a means to identify interactions between specific microbes, environmental parameters and biogeochemical processes (Guidi et al. 2016). Once again, while these approaches have recently provided revolutionary insights into other areas of microbial ecology, they are yet to be brought to bear on questions relating to seagrass microbiology. Consequently, we believe that seagrass microbiology is on the brink of an exciting period of discovery, where a strong conceptual foundation can be built upon with the availability of a powerful new kit of tools, which will ultimately provide a robust platform for deciphering the nature and wider ecological significance of the seagrass microbiome.

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# Chapter 13
# Rhizome, Root/Sediment Interactions, Aerenchyma and Internal Pressure Changes in Seagrasses

**Kasper Elgetti Brodersen, Michael Kühl, Daniel A. Nielsen,**
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**Abstract** Life in seawater presents several challenges for seagrasses owing to low $O_2$ and $CO_2$ solubility and slow gas diffusion rates. Seagrasses have evolved numerous adaptations to these environmental conditions including porous tissue providing low-resistance internal gas channels (aerenchyma) and carbon concentration mechanisms involving the enzyme carbonic anhydrase. Moreover, seagrasses grow in reduced, anoxic sediments, and aerobic metabolism in roots and rhizomes therefore has to be sustained via rapid $O_2$ transport through the aerenchyma. Tissue aeration is driven by internal concentration gradients between leaves and belowground tissues, where the leaves are the source of $O_2$ and the rhizomes and roots function as $O_2$ sinks. Inadequate internal aeration e.g., due to low $O_2$ availability in the surrounding water during night time, can lead to sulphide intrusion into roots and rhizomes, which has been linked to enhanced seagrass mortality. Under favourable conditions, however, seagrasses leak $O_2$ and dissolved organic carbon into the rhizosphere, where it maintains oxic microzones protecting

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the plant against reduced phytotoxic compounds and generates dynamic chemical microgradients that modulate the rhizosphere microenvironment. Local radial $O_2$ loss from belowground tissues of seagrasses leads to sulphide oxidation in the rhizosphere, which generates protons and results in local acidification. Such low-pH microniches can lead to dissolution of carbonates and protolytic phosphorus solubilisation in carbonate-rich sediments. The seagrass rhizosphere is also characterised by numerous high-pH microniches indicative of local stimulation of proton consuming microbial processes such as sulphate reduction via root/rhizome exudates and/or release of alkaline substances. High sediment pH shifts the sulphide speciation away from $H_2S$ towards non-tissue-penetrating $HS^-$ ions, which can alleviate the belowground tissue exposure to phytotoxic $H_2S$. High sulphide production can also lead to iron and phosphorus mobilization through sulphide-induced reduction of insoluble Fe(III)oxyhydroxides to dissolved Fe(II) with concomitant phosphorus release to the porewater. Adequate internal tissue aeration is thus of vital importance for seagrasses as it ensures aerobic metabolism in distal parts of the roots and provides protection against intrusion of phytotoxins from the surrounding sediment.

## 13.1 Introduction

When higher (seed) plants evolved about 400 million years ago, the challenge was to maintain an adequate water balance through the development of a leaf cuticle, stomata, intercellular spaces and xylem, i.e., to become homiohydric (Raven 1977). However, life in air also enables much faster rates of gaseous exchange, since diffusion coefficients for $CO_2$ and $O_2$ are approximately 10,000 times higher in air than in water (Armstrong 1979). When some angiosperms returned to an aqueous environment about 100 million years ago, freshwater hydrophytes and marine seagrasses thus had to overcome constraints on gas exchange imposed by the slower gas diffusion as well as a much lower solubility of $O_2$ and $CO_2$ in water (Table 13.1). Additionally, seagrasses had to contend with mechanical stress such as wave action and other difficulties of living in seawater, for example, ion regulation and sediment-related potential phytotoxins, especially sulphide that occurs in large quantities in marine sediments due to high sulphate levels ($\sim$25 mM) in seawater and the prevalence of sulphate reducing bacteria as a major component in anoxic mineralization of organic material (Jørgensen 1982). Seagrasses show many adaptations found in hydrophytes such as aerenchyma, i.e., airspaces in their tissues providing low-resistance internal gas pathways in both roots and shoots, as well as (i) a photosynthetic leaf epidermis, (ii) loss of stomata, and (iii) reinforced structures to withstand wave-action, such as thick shoot bases and tough strap-shaped leaves (with the major exception of the genus *Halophila* and to some extent *Amphibolis*) (e.g. Armstrong 1979; Larkum et al. 2006a, b).

### 13.1.1 Gas Exchange in Seagrasses

Molecular oxygen ($O_2$) and carbon dioxide ($CO_2$) are substrates and products in respiration and photosynthesis; thus transport processes affecting these gases are of vital importance for seagrasses. The dissolution of $O_2$ in seawater is straightforward, obeying Henry's law, but the dissolution of $CO_2$ is more complex as it is part of the pH-dependent speciation of dissolved inorganic carbon (DIC) in seawater:

$$CO_2 + H_20 \underset{K_{-1}}{\overset{K_{+1}}{\leftrightarrow}} H_2CO_3 \underset{K_{-2}}{\overset{K_{+2}}{\leftrightarrow}} HCO_3^- + H^+ \underset{K_{-3}}{\overset{K_{+3}}{\leftrightarrow}} CO_3^{2-} + 2H^+ \tag{1.1}$$

According to Eq. 1.1, $CO_2$ dissolves in water to form carbonic acid, which is a relatively slow reaction that can be increased by the enzyme carbonic anhydrase (CA) in many biological systems. $H_2CO_3$ at normal pH of seawater (7.5–8.4) disproportionates rapidly into bicarbonate and a proton. At more alkaline pH, bicarbonate disproportionates into carbonate and another proton. The action site of CA is indicated in Eq 1.1 by a grey box. CA can be located both intra- and extra-cellularly (e.g. Badger and Price 1994) and there is good evidence in many photosynthetic systems for the secretion of extracellular CA into the cell wall facilitating an enhanced uptake of $CO_2$ via $HCO_3^-$ conversion (e.g. Badger and Price 1994). The presence of CAs in seagrasses has been much debated but their presence had until recently only been inferred by inhibitor studies (e.g. Larkum and James 1996; Beer et al. 2002). However, CA coding genes have now been found to be expressed in the transcriptome of *Zostera muelleri* spp. *capricorni* (Golicz et al. 2015). Although the precise location of CA in the seagrass tissue has not been resolved, previous evidence indicated their presence in the outer cell wall of the leaf epidermal layers of many seagrasses (Larkum and James 1996; Beer et al. 2002; Borum et al. 2015).

It appears that seagrasses have developed mechanisms to enhance the uptake of DIC (Beer et al. 2002; Larkum et al. 2006a, b), and such mechanisms are discussed in detail in Chap. 16. For the present purpose, it is enough to know that photosynthetic carbon fixation is facilitated by several mechanisms that either passively or actively transports DIC from the surrounding seawater into the cytoplasm and chloroplasts of the epidermal cells, where $CO_2$ fixation takes place and $O_2$ is

**Table 13.1** Concentration and diffusion coefficients of $O_2$, $CO_2$ and bicarbonate ion in air and air-saturated seawater (salinity of 35) at a temperature of 25 °C (Larkum et al. 1989)

| | Concentration (mmol $m^{-3}$) | | | Diffusion coefficients ($m^2$ $s^{-1}$) | | |
|---|---|---|---|---|---|---|
| | $CO_2$ | $HCO_3^-$ | $O_2$ | $CO_2$ | $HCO_3^-$ | $O_2$ |
| Air | 17 | 0 | 9375 | $1.56 \times 10^{-5}$ | NR | $1.97 \times 10^{-5}$ |
| Seawater | 11.5 | 2000 | 206 | $1.55 \times 10^{-9}$ | $1.00 \cdot 10^{-9}$ | $2.26 \times 10^{-9}$ |

Data is calculated based upon an atmospheric $CO_2$ concentration of 401 ppm

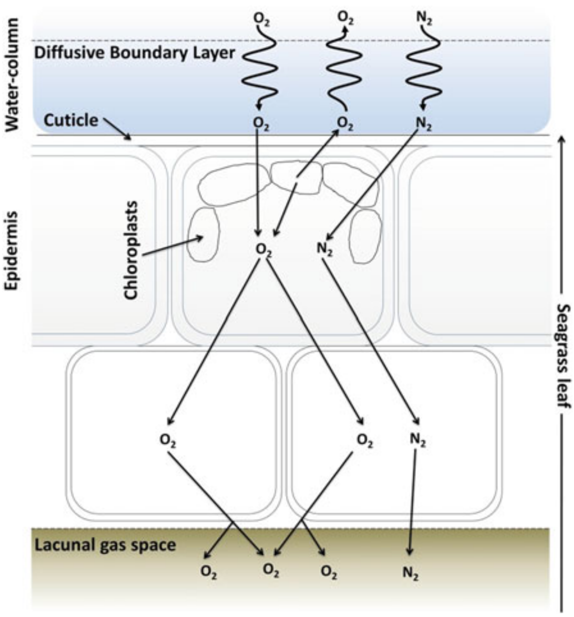

**Fig. 13.1** Conceptual diagram showing the major diffusional transport routes for $O_2$ and $N_2$ from the ambient medium to the lacunal space (under non-pressurised conditions) in a seagrass leaf. Data modified from Larkum et al. (1989)

produced. Photosynthesis-generated $O_2$ moves via diffusion to either the surrounding seawater or inwards from the epidermal cells into the surrounding tissue and the aerenchymal spaces depending on the actual concentration gradient and the resistance to diffusion (Fig. 13.1; e.g. Colmer 2003).

An important consideration for the movement of gases in seagrasses is the diffusional constraints on the movement of $CO_2$ and $O_2$ both in solution and in the gas phase (Larkum et al. 1989, 2006a, b). The diffusive gas transport is described by Fick's first law:

$$J_j = D_j(C_a - C_s)/l \tag{1.2}$$

where $J_j$ is the flux of gas j (mol $m^{-2}$ $s^{-1}$), $D_j$ is the diffusion coefficient of the gas j ($m^2$ $s^{-1}$) (in water or in air; at a given temperature and salinity), l is the distance over which diffusion occurs (m), $C_a$ and $C_s$ are the concentrations of the gas j (mol $m^{-3}$) at the source and sink, respectively. In this formulation it is assumed that there is (i) a net flux of gas from source to sink, (ii) no net consumption or production of the diffusing species underway, and (iii) that $C_a$ and $C_s$ are constant—see Nobel (1990). In the following sections, $O_2$ will mainly be expressed as a concentration (in μmol $L^{-1}$) when in solution and as a partial pressure (in kPa) when in the gas phase; where ~240 μmol $L^{-1}$ (depending on salinity and temperature) and ~20.6 kPa represents 100% air saturation in a marine environment.

The diffusive transport of a gas across a given plant tissue compartment can be conceptualized as a set of electrical resistances in series (and parallel) (Van den Honert 1948; Raven 1977; Armstrong 1979; Nobel 1990):

$$J_j = D_j(C_a - C_s)/l = DF/R_{jT} \tag{1.3}$$

where $D_j/l = 1/R_{jT}$ and $R_{jT}$ is the total resistance of the gas transport pathway to species j, having the units, s $m^{-1}$. DF is the driving force or the concentration gradient ($C_a$–$C_s$). And each component of the pathway (catenary) can be assigned as previously described in Larkum et al. (1989):

$$J_j = DF/R_{jT} = DF_a/R_{ja} = DF_b/R_{jb} = DF_c/R_{jc},\ \text{etc.} \tag{1.4}$$

and therefore

$$R_{jT} = R_{ja} = R_{jb} = R_{jc},\ \text{etc.} \tag{1.5}$$

where the subscripts T, a, b, c, etc. refer to the total sequence of diffusional steps (T = total) and to the individual steps (a, b, c, etc.); for example, a represents the diffusive boundary layer, b the cuticle, c the epidermal cell wall, etc. (Fig. 13.1).

Using this formulation, it is possible to set out a resistance circuit for the movement of $CO_2$ and $O_2$ across the epidermal cell and hypodermal cell of a seagrass, respectively. Such a formulation can then be used to calculate the flux of $O_2$ either outwards from the epidermal cell or inwards into the aerenchymal spaces (Fig. 13.1; see Larkum et al. 2006a, b) and as we show in the next section, this has important implications for our understanding of the aeration of seagrasses.

### *13.1.2 Diffusive Boundary Layers and Water Motion Around Seagrass Leaves*

Gas exchange between aquatic macrophytes and the surrounding water is impeded by the presence of a diffusive boundary layer (DBL) (e.g. Jørgensen and Revsbech 1985; Hurd 2000; Brodersen et al. 2015a). As flow declines towards the plant surface, the viscosity of water dampens out turbulences, forming the DBL as a thin layer of water just above the tissue surface where molecular diffusion governs solute exchange between tissue and water. The thickness of the DBL is affected by water flow and surface rugosity (e.g. Jørgensen and Des Marais 1990; Larkum et al. 2003), where low flow and/or more coarse topography lead to a thicker DBL than fast flow and/or a more smooth surface. The DBL thickness is an important factor controlling solute exchange as diffusion time increases with the square of the DBL thickness. Therefore, the DBL can present a major barrier to plant solute exchange, especially under low flow conditions or e.g. in the presence of epiphytes on seagrass leaves that increase rugosity (Brodersen et al. 2015a). Larkum et al. (1989)

**Table 13.2** Gaseous composition of the lacunal system of several seagrasses (Larkum et al. 1989)

| Species | $O_2$ (%) | $N_2$ (%) | $CO_2$ (%) | % of $O_2$ flux to lacunae | Max. lacunal pressure (kPa) |
|---|---|---|---|---|---|
| *Zostera muelleri* subsp. *capricorni* | 32.3 | 67.6 | – | 13 | – |
| *Cymodocea serrulata* | 34.3 | 65.4 | 0.0095 | 16 | 22.0 |
| *Syringodium isoetifolium* | 32.2 | 64.4 | 0.140 | 17 | 8.18 |
| *Halophila ovalis* | 34.1 | 66.1 | – | – | 10.0 |
| *Enhalus acoroides* | 33.5 | 67.0 | 0.1017 | 12.6 | – |
| *Amphibolis antarctica* | 31.7 | 67.8 | – | 8 | – |
| *Halodule uninervis* | – | – | 0.0037 | – | – |

reported a DBL thickness on seagrass leaves ranging from ~50 μm under maximal flow to 200–1000 μm under medium to low flow conditions, and this range was later confirmed by microsensor measurements (e.g. Binzer et al. 2005; Borum et al. 2006; Brodersen et al. 2015a). For seagrasses, this means that under natural conditions there will be a strong diffusion resistance to movement of solutes into the leaves from the surrounding seawater (Fig. 13.1).

With respect to $O_2$, the DBL at the outer surface of the leaves means that, despite the proximity of the epidermal cell layer to the surrounding seawater, the diffusion resistance for molecules moving out of the epidermis or into the airspace system of the aerenchyma can be similar. Thus, during medium to high light exposure, when photosynthesis is active and $O_2$ is being produced at high rates, accumulating $O_2$ pressurizes the aerenchyma (Table 13.2; Larkum et al. 1989; Bodensteiner 2006). This can be seen in many seagrass species where, around midday, the leaves become more erect, and gas bubbles can often be seen escaping from wounds in the leaf surface. The pressurisation of the leaf during active photosynthesis leads to increased $O_2$ partial pressure ($pO_2$), which may increase $O_2$ supply to the roots and rhizome. However, the longitudinal transport to the below-ground tissues is greatly restricted by the diminished aerenchymal spaces in the shoot base manifold (further described in Sect. 13.2).

## 13.2 Internal Aeration

The leaves of seagrasses are generated at the base of the shoot, i.e., the basal leaf meristem that in mono-meristematic leaf-replacing species such as *Zostera* and *Posidonia* is a combined rhizome/basal leaf meristem area at the root-shoot junction (Fig. 13.2). Three other forms exists, i.e., di-meristematic leaf-replacing species (such as *Thalassia* and *Cymodocea*), mono-meristematic non-leaf-replacing species (mostly *Halophila*), and di-meristematic non-leaf-replacing species (few species of *Halophila*) (e.g. Short and Duarte 2001), but in the following we will mainly focus

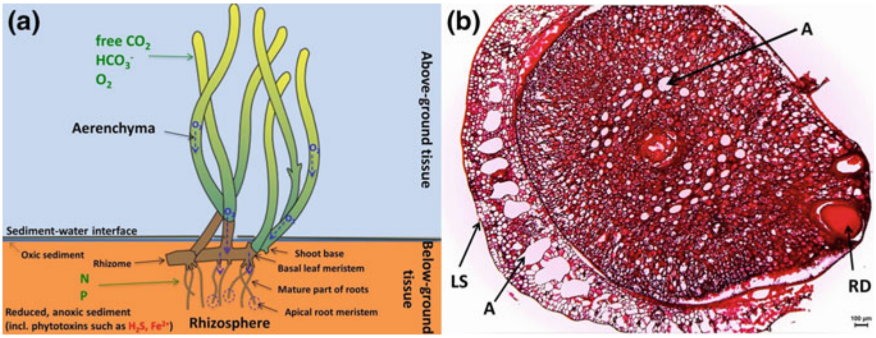

**Fig. 13.2** **a** Conceptual diagram of the aerenchymal system in seagrass. **b** Cross-sectional image of a shoot base with leaf sheath of *Zostera muelleri* spp. *capricorni* showing the extended air lacunal system at the meristematic region of the rhizome. Scale bar = 100 µm. LS = indicate the leaf sheath; A = aerenchyma; RD = initial root development. Data modified from Brodersen et al. (2015b). Copyright 2015 John Wiley & Sons Ltd.

on the mono-meristematic leaf-replacing species. The meristematic region of the rhizome has poorly developed aerenchyma owing to the compact anatomy of the tissue, and thereby $O_2$ diffusion to this area is impeded. To alleviate this structural limitation to $O_2$ movement, the surrounding leaf sheath has an extensive distribution of large, internal gas channels (Fig. 13.2). The shoot base also produces fiber-rich tissue that provides biomechanical strengthening of the root/shoot base against wave action, and many seagrasses also have adventitious roots that anchor the shoot base into the sediment. As a consequence, the aerenchyma system, which consists of long gas channels or lacunae that stretch through the leaves and roots, peter out in the shoot base, where it is replaced by a much more tenuous intercellular pathway for gas transport (Fig. 13.2). The net result of this extended and reinforced gas pathway in the shoot base manifold causes $O_2$ to diffuse laterally into the surrounding sediment and tissues, especially to the young developing leaves in addition to the downwards diffusion to the rhizome and roots (e.g. Pedersen et al. 1998, 1999; Jensen et al. 2005; Frederiksen and Glud 2006; Brodersen et al. 2014; Koren et al. 2015; Brodersen et al. 2015a, b). Hence, while the root/shoot manifold forms a hindrance to the passage of $O_2$ from shoot to root, it alleviates mechanical stress from wave action and secures the $O_2$ supply to the young meristematic tissues, thereby enabling a protection against intrusion of sediment-produced $H_2S$.

### 13.2.1 Internal $O_2$ Concentration Gradients

The sediment surrounding the rhizosphere is largely anoxic and thus roots and rhizomes are unable to take up $O_2$ from the sediment environment. Instead, $O_2$ moves along a concentration gradient from the above-ground shoot to the rhizome and root-tips by means of molecular gaseous diffusion. As described above, diffusion in the liquid phase is slow and not effective over distances larger than a few mm. As a consequence, seagrasses have evolved a network of porous gas-filled spaces (aerenchyma) in all tissues where gas phase diffusion enables sufficient $O_2$ transport to the below-ground tissues.

The driving force of $O_2$ transport is the strong internal gradient in $O_2$ partial pressure ($pO_2$) from shoot to root tip. The gradient develops as a result of (i) $O_2$ consumption of the tissues, and (ii) radial $O_2$ loss (ROL) from the aerenchyma to the environment. In the mature zones of rhizomes and roots, tissue respiration is moderate since the metabolic processes primarily serve to support maintenance respiration, and barriers to ROL exists that reduce the loss of $O_2$ along the diffusion pathway (Colmer 2003). In the apical zones of rhizomes and in the root-tips, on the other hand, cell division requires additional energy and thus increased $O_2$ consumption, resulting in a steep decline in tissue $pO_2$. The root-tips are highly permeable to $O_2$ and ROL is extensive (Jensen et al. 2005; Pedersen et al. 1998), resulting in a steep gradient in $pO_2$ inside the aerenchyma from shoot to root-tip. This gradient drives a steady flux of $O_2$ to the $O_2$ demanding tissues. Figure 13.3 demonstrates how tissue $pO_2$ systematically declines with distance to the shoot, which acts as entry point of $O_2$ in the dark and a site of $O_2$ production in the light.

In the dark, the $pO_2$ of roots and rhizomes is strongly correlated to water-column $pO_2$ (e.g. Greve et al. 2003), which is reflected by decreasing tissue $pO_2$ following a decline in water-column $pO_2$ (Fig. 13.3). A strong dependence of water-column $O_2$ on the night-time tissue respiration has also been demonstrated in situ (Sand-Jensen et al. 2005; Borum et al. 2005). Sand-Jensen et al. (2005) reported that at dusk, when photosynthesis ceased ($\sim$8 p.m., Fig. 13.4), tissue $pO_2$ declined rapidly to a point where the decline followed water-column $pO_2$ (Fig. 13.4), and the shoot base

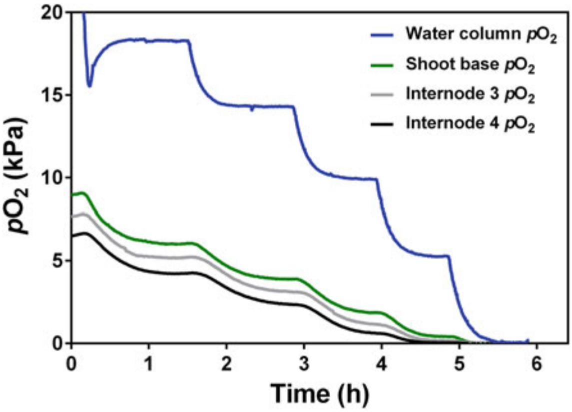

**Fig. 13.3** Below-ground tissue $pO_2$ as a function of water-column $pO_2$ in darkness measured in *Zostera marina*. The $O_2$ microelectrodes were inserted into the shoot base close to the leaf meristem, which was buried approximately 5 mm into the sediment, and in the 3rd and the 4th internode of the rhizome. The $pO_2$ of the water-column was successively reduced in steps of 4–5 kPa over a timeframe of 6 h and kept at 20 °C. Data modified from Pedersen et al. (2004)

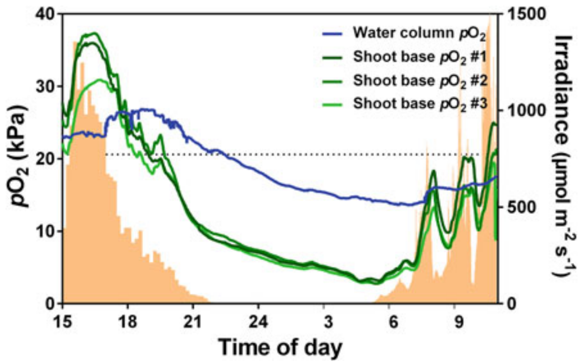

**Fig. 13.4** In situ $pO_2$ of the shoot base of 3 replicate plants of *Zostera marina* and the water-column over a diurnal cycle measured in Roskilde Fjord, Denmark. The $O_2$ microelectrodes were inserted into the shoot base close to the leaf meristem, which was buried approximately 5 mm into the sediment. The dotted line indicates air equilibrium of dissolved $O_2$. Irradiance of the PAR spectrum (400–700 nm) measured at the canopy surface is shown in orange colour. Data modified from Sand-Jensen et al. (2005)

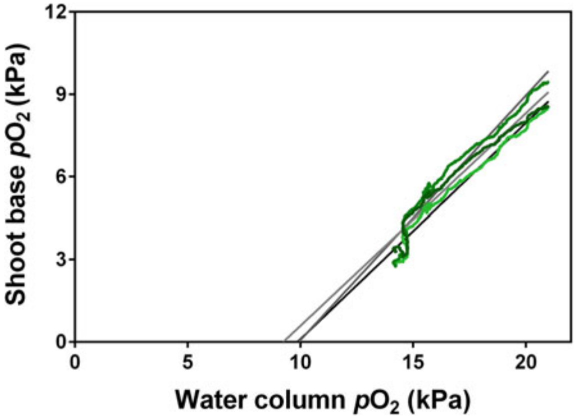

**Fig. 13.5** Water-column $pO_2$ versus shoot base $pO_2$ during night-time of 3 replicate plants of *Zostera marina*. The data are extracted from Fig. 13.4 in the time period of 10 p.m. to 5 a.m. The grey lines represent linear regression of each replicate plant and are extrapolated to interception with the horizontal axis (as this gives an estimate of at which water-column $pO_2$ the vulnerable shoot base tissue becomes anoxic). Data modified from Borum et al. (2006)

became anoxic at a water-column $pO_2$ of approximately 9–10 kPa ($\sim$50% air saturation; Fig. 13.5). The water-column $pO_2$ required to prevent shoot base anoxia depends on the above-ground:below-ground tissue ratio since the shoot acts as site of $O_2$ uptake, whereas roots and rhizomes are sinks due to respiration and ROL. At a relatively low ratio, the critical water-column $pO_2$ for shoot base anoxia would be higher compared to a situation, where the ratio is higher. Implications of tissue anoxia encompass (i) low energy yield when anaerobic fermentation takes over from respiration, (ii) reduced nutrient uptake by the roots, (iii) impeded translocation of carbohydrates and nutrients between leaves and roots, and (iv) anoxic rhizosphere conditions near the root-tips potentially leading to sulphide intrusion (see below; e.g. Zimmerman and Alberte 1996; Pedersen et al. 2004; Borum et al. 2006; Brodersen et al. 2015b).

The aerenchyma has been suggested to function as an important reservoir of $O_2$ for respiration in the dark. However, in the case of *Z. marina*, the pool of $O_2$ initially captured in the aerenchyma would only be able to support respiratory demands for 8–13 min, assuming an initial $pO_2$ near atmospheric equilibrium (i.e. 20.6 kPa) (Sand-Jensen et al. 2005). Moreover, shoot and apical root tissues are highly gas permeable and the pool of $O_2$ quickly equilibrates with the environment (e.g. Fig. 13.3) further shortening the time that stored $O_2$ can meet respiratory demands. Thus, seagrasses primarily rely on a reservoir of $O_2$ in the water-column surrounding the leaves to support night-time respiration in their tissues, and this makes them vulnerable to $O_2$ depletion in the water-column during night-time or periods of low irradiance, e.g. due to low water transparency.

Photosynthetically produced $O_2$ supports daytime respiration in both above- and below-ground seagrass tissues. In the light, shoot base tissue $pO_2$ can reach 40 kPa or more (Fig. 13.4) and thereby significantly exceed water-column $pO_2$. As previously mentioned, the high tissue $pO_2$ in the leaves in the light results in a steep $O_2$ gradient to the surrounding water-column and also internally from shoot to root-tips. This facilitates that even the most distant root-tips can experience daytime $pO_2$ of close to air equilibrium as shown for e.g., *Cymodocea rotundata* and *Zostera marina* (Jensen et al. 2005; Pedersen et al. 1998).

The strong relationship between below-ground tissue $pO_2$ and photosynthesis during the day is illustrated in Fig. 13.6 showing a saturation of shoot base $pO_2$ with increasing irradiance (measured at leaf canopy height) with a shape resembling typical photosynthesis *versus* irradiance curves. The data for Fig. 13.6 are extracted from the light period between 6 and 11 a.m. in Fig. 13.4, and show that with a

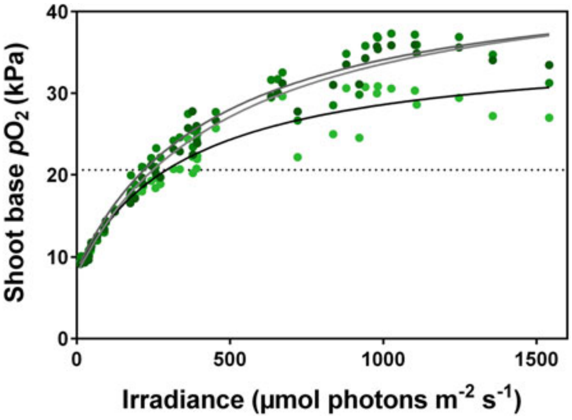

**Fig. 13.6** Irradiance versus shoot base $pO_2$ during day-time of 3 replicate plants of *Zostera marina*. The data are extracted from Fig. 13.4 in the time period of 6 p.m. to 11 a.m. on day 2. The grey lines represent non-linear regression of each replicate plant applying a Jassby and Platt (1976) model. The dotted line represents air saturation of dissolved $O_2$. Data modified from Borum et al. (2006)

photon irradiance of approximately 250–300 μmol photons $m^{-2}$ $s^{-1}$ and above, shoot base $pO_2$ exceeds the atmospheric equilibrium of 20.6 kPa. Thus, in shallow transparent waters governing good light conditions, the below-ground tissues of seagrasses exhibit a beneficial intra-plant $O_2$ status due to photosynthetic $O_2$ production during the day.

## 13.3 Seagrass-Sediment Interactions

Seagrasses are generally found in highly reduced sediments enriched with organic matter (Borum et al. 2006) including remnants of seagrass plants. The high productivity of seagrass meadows and the resulting continuous contribution of organic matter to the sediment, both from seagrass debris and exudates from roots and rhizomes (Moriarty et al. 1986; Pollard and Moriarty 1991), as well as from enhanced sedimentation due to diminished flow in dense seagrass beds (Ward et al. 1984; Madsen et al. 2001), supports high rates of microbial carbon mineralization in the sediment. The $O_2$ solubility in seawater is limited (typically 284–196 μM in air-saturated seawater at 10–30 °C and a salinity of 34) as compared to terrestrial systems, and the $O_2$ supply to the sediment from the seawater can be impeded by the diffusive boundary layer (DBL) (e.g. Jørgensen and Revsbech 1985; Jørgensen and Des Marais 1990; Kühl and Revsbech 2001) and slow internal sediment diffusion rates (Glud et al. 2007). Aerobic respiration and re-oxidation of reduced chemical species diffusing towards the sediment-water interface rapidly deplete $O_2$ in the upper mm's of the sediment. In anoxic marine sediments, microbial sulphate reduction is the dominant anaerobic respiratory process (Jørgensen 1982), whereby sulphate is reduced to sulphides that exhibit a pH dependent speciation (with a $pK_a$ value of ~pH 7) into dissolved hydrogen sulphide gas ($H_2S$) and hydrogen sulphide ions ($HS^-$) at typical sediment pH values. Sulphide species react efficiently with oxidized molecules such as Fe(III), causing a further reduction of the sediment. Due to its high toxicity to aerobic organisms, high $H_2S$ concentrations are generally detrimental to plants and animals living in sulphidic sediments (Lamers et al. 2013). It has therefore long been speculated that seagrasses must have a capacity to alleviate $H_2S$ exposure in order to sustain their own growth.

### 13.3.1 *$H_2S$ Intrusion at Low Water-Column $O_2$ Concentrations*

Water-column hypoxia during night-time can lead to $H_2S$ intrusion into below-ground tissues if the $O_2$ flux across the DBL is insufficient to maintain ROL at the basal leaf meristem and root-tips. The fast growing root-tips are highly gas permeable because they lack a structural barrier to ROL (Connell et al. 1999),

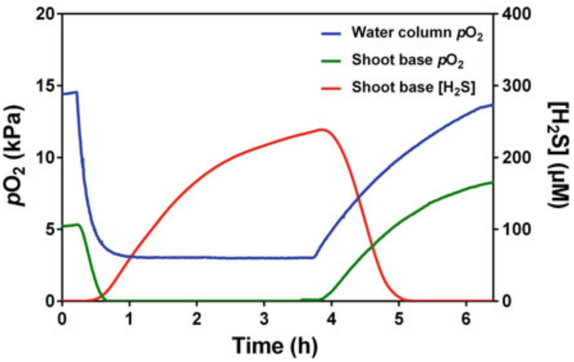

**Fig. 13.7** Shoot base $pO_2$ and shoot base $H_2S$ as a function of water-column $pO_2$ in *Zostera marina*. The $O_2$ and $H_2S$ microelectrodes were inserted into the shoot base close to the leaf meristem, which was buried approximately 5 mm into the sediment. Water-column $pO_2$ was manipulated in steps of about 10 kPa and kept at 20 °C. Data modified from Pedersen et al. (2004)

but during conditions with normal water-column $pO_2$, the ROL results in the formation of a so called "oxic microshield" in the rhizosphere around the basal leaf meristem and root-tips (Jensen et al. 2005; Frederiksen and Glud 2006; Brodersen et al. 2015b). The released $O_2$ can oxidize sulphide and thereby prevent $H_2S$ from diffusing into the young, structurally unprotected tissue (further described in Sect. 13.3.2 below; Brodersen et al. 2015b). During water-column hypoxia, however, the ROL may become insufficient to maintain these oxic shields in the rhizosphere, increasing the risk of $H_2S$ exposure and intrusion (Fig. 13.7).

Gaseous $H_2S$ spreads by molecular diffusion inside the aerenchyma from areas of high concentration near the root-tips towards the shoot. In the gas phase, oxidation of $H_2S$ with $O_2$ is a relatively slow spontaneous chemical reaction, and both $O_2$ and $H_2S$ can thus coexist for some time in the same tissues (Borum et al. 2005; Pedersen et al. 2004). Figure 13.7 shows an example, where water-column $pO_2$ was experimentally manipulated, and where a decline from 15 to 3 kPa $O_2$ resulted in $H_2S$ intrusion. At the shoot base, $H_2S$ was detected in the tissue before complete $O_2$ depletion, where after $H_2S$ continued to rise up to ~250 µM. When the surrounding water-column was brought back to atmospheric equilibrium, $pO_2$ in the shoot base increased, while $H_2S$ was depleted. However, $O_2$ and $H_2S$ co-existed in the same tissue for >1 h until $O_2$ reached the root-tips, and $H_2S$ intrusion was once again restricted by the oxic sediment microshield. Recent studies also suggest an internal $H_2S$ detoxification mechanism, whereby $H_2S$ is oxidized to elemental sulphur (an intermediate in sulphide oxidation) precipitating on the inner walls of the aerenchyma (e.g. Holmer and Hasler-Sheetal 2014; Hasler-Sheetal and Holmer 2015).

Intrusion of $H_2S$ into seagrass tissue has also been demonstrated in situ, where sulphide poisoning has been suggested to result in localised die-off events (e.g. Borum et al. 2005; Carlson Jr et al. 1994). Florida Bay in the U.S. has been severely affected by such die-off events, and Borum et al. (2005) showed that gaseous $H_2S$

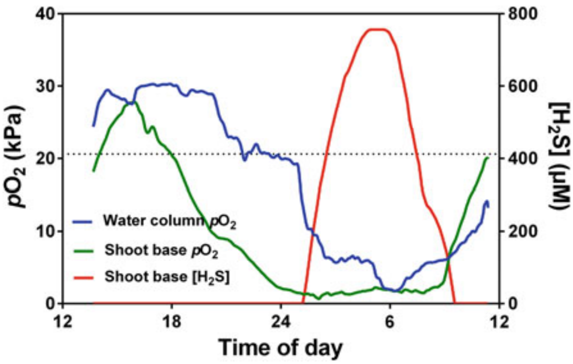

**Fig. 13.8** In situ $pO_2$ and $H_2S$ of the shoot base of *Thalassia testudinum* and the water-column $pO_2$ over a diurnal cycle measured in a die-off patch at Barnes Key, Florida Bay, USA. The $O_2$ and $H_2S$ microelectrodes were inserted into the shoot base close to the leaf meristem, which was buried approximately 20 mm into the sediment. The dotted line indicates air equilibrium of dissolved $O_2$. Data modified from Borum et al. (2005)

started penetrating the below-ground tissues and spread to the shoot base of seagrasses at a water-column $pO_2$ of approximately 50% air equilibrium (10 kPa) (Fig. 13.8). As the water-column experienced further hypoxia during the night, $H_2S$ reached a tissue concentration of more than 750 µM in the shoot base. In line with the observations from laboratory experiments (Fig. 13.7), the shoot base never became anoxic and $H_2S$ and molecular $O_2$ coexisted throughout the night (Fig. 13.8). Tissue $H_2S$ then started declining following sunrise, as photosynthetically produced $O_2$ resulted in higher $pO_2$ in the below-ground tissues, but $H_2S$ persisted in the shoot base tissue until 10 a.m., i.e., >4 h after sunrise. Sulphide intrusion into the below-ground tissue of seagrasses is thus strongly linked to the $O_2$ status of the plants.

Koren et al. (2015) found that the oxygenated region around the seagrass rhizome of *Z. muelleri* was diminished during night-time (Fig. 13.9), likely in response to lowering of the internal $pO_2$ and thereby a reduction in the $O_2$ gradient from the rhizome to the anoxic sediment. A combination of darkness and low water-column $pO_2$ ($\sim$50% air equilibrium) has previously been shown to enable $H_2S$ to reach the root and rhizome of the plant, thus exposing the plant to potential poisoning (Fig. 13.10). Seagrasses may thus be sensitive to diminished water flow, light and/or pollution that can affect the $O_2$ transport to the lower tissue regions of the plant. Pollution effects include sediment re-suspension from dredging, which lowers the photosynthetically active radiation (PAR) reaching the leaves (Erftemeijer and Lewis 2006), and eutrophication-induced algal blooms lowering light availability and water-column $O_2$ concentrations through increased night-time respiration and degradation of settled algal biomass in the sediment. Growth of epiphytic algae on the seagrass leaf can also reduce PAR and increase the DBL thickness and thereby impede $O_2$ transport into the leaf (Drake et al. 2003; Brodersen et al. 2015a).

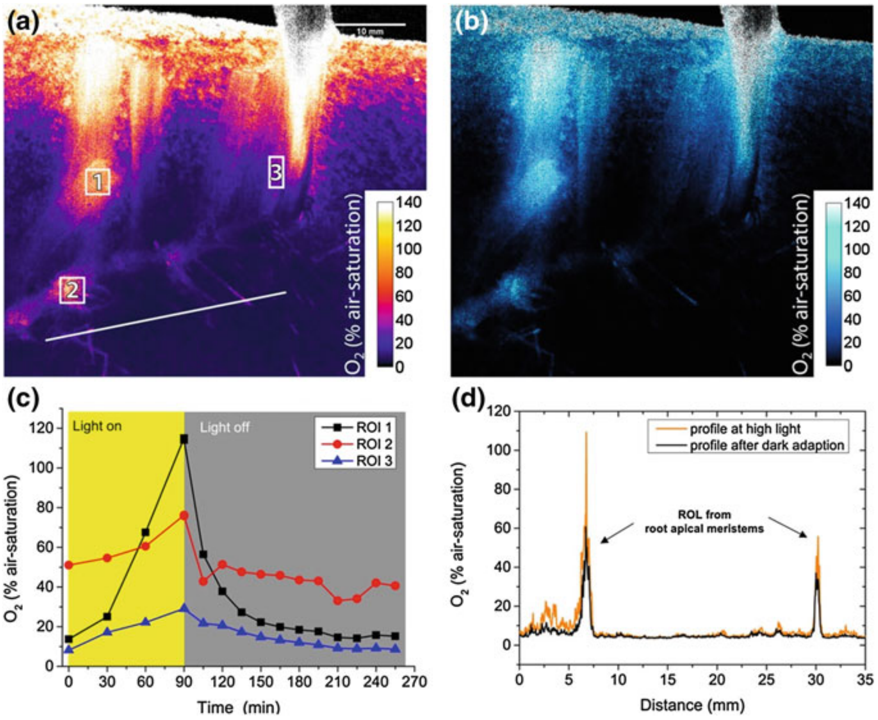

**Fig. 13.9** **a** Colour coded $O_2$ image acquired via novel optical nanoparticle-based $O_2$ sensors, visualising the $O_2$ distribution in the seagrass rhizosphere under an incident photon irradiance of 500 µmol photons $m^{-2}$ $s^{-1}$. **b** The relative difference in the below-ground tissue oxidation capacity between measurements in light and darkness. **c** Real-time $O_2$ concentrations within selected regions of interest (ROIs, as shown in panel A) during a light/dark transition. Black symbols and profile represents measurements at the prophyllum (ROI 1), red symbols and profile represent measurements at the root-shoot junction (ROI 2), blue symbols and profile represent measurements at the basal leaf meristem (ROI 3). **d** The extracted line profile from the $O_2$ image (shown in panel A) across 2 roots, visualising radial $O_2$ loss (ROL) from the root apical meristems during a light/dark transition. Partly redrawn with permission from Koren et al. (2015). Copyright 2015 American Chemical Society

## *13.3.2 Oxic Microshields and Below-Ground Tissue Oxidation Capacity*

The passive, internal aeration system of the seagrass plant not only serves to aerate various tissue parts including the below-ground portions (see Sects. 13.1 and 13.2). Aerenchymatic gas transport to the below-ground tissue and ROL to the surrounding sediment enables oxidation of the immediate rhizosphere microenvironment and alleviates exposure to phytotoxins such as $H_2S$ (Brodersen et al. 2015b). The release of $O_2$ from roots and rhizomes has been demonstrated on multiple occasions

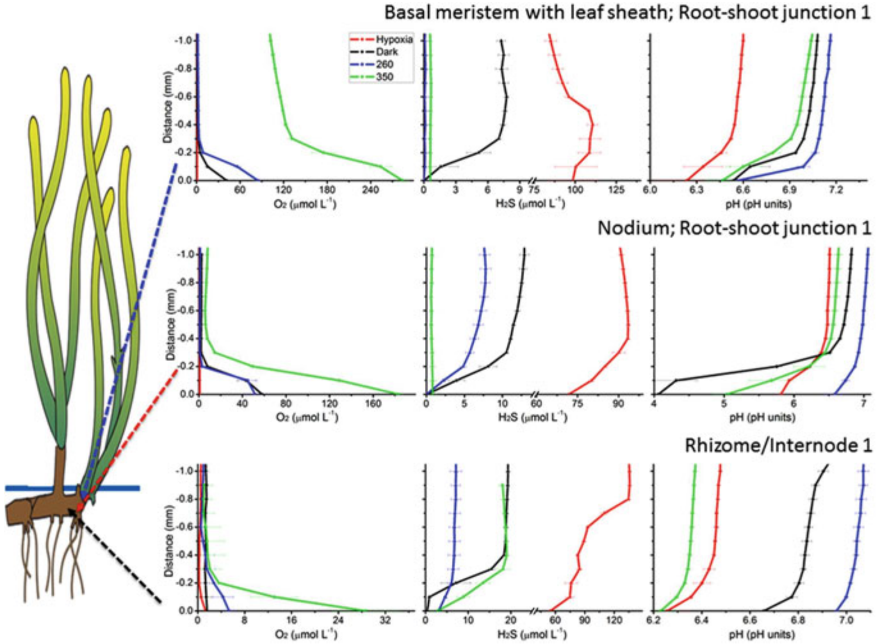

**Fig. 13.10** Seagrass-derived sediment detoxification as a result of below-ground tissue radial $O_2$ loss into the immediate rhizosphere. Concentration profiles of $O_2$, $H_2S$ and pH were measured with microelectrodes in darkness (black profiles), at an incident photon irradiance of 260 (blue profiles) and 350 (green profiles) µmol photons $m^{-2}$ $s^{-1}$, and in darkness with hypoxic conditions in the water-column (red profiles). *Upper panels* represents measurements at the basal leaf meristem with leaf sheath, *intermediate panels* (horizontally) at the root-shoot junction and *lower panels* at the rhizome. *Left panels* represent the immediate rhizosphere $O_2$ concentration, *intermediate panels* (vertically) represents the immediate rhizosphere $H_2S$ concentration and *right panels* represents the immediate rhizosphere pH. Y = 0 indicate the below-ground tissue surface. Error bars are ±SD. n = 2–4. Note the break on the x-axis of panels illustrating the immediate rhizosphere $H_2S$ concentration. The illustration of *Z. muelleri spp. capricorni* originates from the IAN/UMCES symbol and image libraries (Diana Kleine, Integration and Application Network (IAN), University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)). Data modified from Brodersen et al. (2015b). Copyright 2015 John Wiley & Sons Ltd.

(Pedersen et al. 1998, 1999; Jensen et al. 2005; Frederiksen and Glud 2006; Brodersen et al. 2015a, b; Jovanovic et al. 2015; Koren et al. 2015) (Fig. 13.9), but only recently has the direct connection between $O_2$ release and removal of $H_2S$ around the below-ground tissue been confirmed (Brodersen et al. 2014, 2015b). By applying a split flow chamber with artificial, transparent sediment, Brodersen and co-workers used microsensors to measure the $O_2$ release from the below-ground tissue from *Z. muelleri* spp. *capricorni* and could align such oxic microzones with the concomitant detection of $H_2S$ depletion towards the roots and rhizomes resulting from chemical oxidation (Fig. 13.10). While the leakage of $O_2$ varied across the rhizome, a several hundred µm thick oxic microshield was detected at the point of

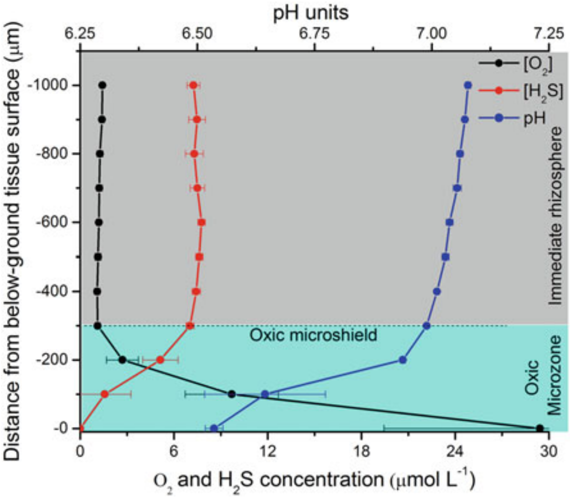

**Fig. 13.11** Oxic microshields surrounding the root/shoot junctions (including the basal leaf meristem with leaf sheath), the rhizome and the apical root meristems of seagrasses. Black symbols and profile represents [$O_2$]; red symbols and profile represents [$H_2S$]; and blue symbols and profile represents pH. The shown microelectrode microprofiles are from the meristematic region of the rhizome. Y = 0 indicate the below-ground tissue surface. Error bars are ±SD. n = 3. Data modified from Brodersen et al. (2015b). Copyright 2015 John Wiley & Sons Ltd.

radial $O_2$ loss (Fig. 13.11), which was sufficient to oxidize most of the $H_2S$ before it reached the tissue surface (Figs. 13.10 and 13.11).

In contrast to previous observations in temperate *Z. marina* plants (Jensen et al. 2005), *Z. muelleri*, which extends into subtropical regions, showed no or very little ROL from the root-tips, and the highest ROL was found around the basal leaf meristem with leaf sheaths, where new leaves are generated (Brodersen et al. 2014, 2015b; Koren et al. 2015). While mature seagrass tissue has a high resistance to radial $O_2$ transport (Jensen et al. 2005; Frederiksen and Glud 2006) partly due to the presence of Casparian-band like structures (Barnabas 1996), the new tissue being formed in the meristem has a poorly developed lacunal system and little resistance to radial gas transport. As such, the concomitant higher lateral movement of $O_2$ to the meristematic tissue of *Z. muelleri* is likely an adaptation to protect this crucial but vulnerable tissue of the plant against exposure to $H_2S$, both internally and externally. However, to what extent this is a general feature of seagrasses needs further evaluation.

Anoxic, reduced sediment conditions have also been shown to induce development of below-ground tissue gas barriers owing to accumulation of suberin lamellae in the hypodermal tissue of seagrasses (Enstone et al. 2003; Armstrong and Armstrong 2001, 2005). Adequate internal aeration is thus a key prerequisite for healthy seagrass communities, as the intra-plant $O_2$ status and thereby the below-ground tissue oxidation capacity to a large extent determines the resilience of the plants towards sediment-produced $H_2S$ and environmental disturbances, such as nutrient loadings and dredging operations leading to markedly reduced light availability and $O_2$ conditions in the water-column (Brodersen et al. 2015a, b).

Apart from its protective function, ROL into the rhizosphere may also stimulate aerobic heterotrophic bacteria leading to increased local remineralisation and mobilization of nutrients of potential benefit to the seagrasses (Blaabjerg et al. 1998; Brodersen et al. 2017a; Hansen et al. 2000; Nielsen et al. 2001) (see also Chap. 17). Nutrient mobilization can also happen through a change in the rhizosphere pH as a result of ROL (Brodersen et al. 2017a). Brodersen et al. (2015b) showed that the pH microenvironment around the below-ground tissue was affected by ROL with pH decreasing by 1–2 pH units inside the oxic microshield relative to the surrounding buffered, artificial sediment (Fig. 13.10). This drop in pH is likely a result of the release of protons ($H^+$) from re-oxidation of $H_2S$, and this mechanism has been proposed to be of significance for the mobilization of phosphate in carbonate-rich sediments (Fourqurean and Zieman 2002; Holmer et al. 2006; Brodersen et al. 2015b; Brodersen et al. 2017a).

### *13.3.3 Rhizosphere pH Heterogeneity and pH-Mediated Sulphide Detoxification*

While seagrass $O_2$ dynamics has been investigated in several studies, much less is known about spatio-temporal pH dynamics in the seagrass rhizosphere. By means of novel nanoparticle-based optical pH imaging, Brodersen et al. (2016) recently documented pronounced spatio-temporal pH heterogeneity in the immediate rhizosphere of the seagrass *Z. marina* L. Imaging of the sediment pH distributions in 2D revealed several distinct micro-niches of low and high pH within the seagrass rhizosphere as compared to the bulk sediment pH (Fig. 13.12). Light exposure of the canopy and an experimental temperature increase from 16 to 24 °C, i.e., to the temperature optimum for oxygenic photosynthesis in summer acclimated *Z. marina* L. plants (Staehr and Borum 2011), lead to elevated pH levels in the seagrass rhizosphere with rhizome/root surface pH increasing by up to 0.9 pH units relative to the sediment pH. This photosynthesis/temperature-dependent pH effect may be due to: (i) secretion of allelochemicals like amines by the plant, (ii) $CO_2$ uptake by the below-ground tissue changing the carbonate equilibrium in the rhizosphere (Colmer 2003; Larkum unpublished data), and/or (iii) enhanced root/rhizome exudates stimulating sulphate reducing bacteria in the rhizoplane consuming protons through their microbial metabolism (Pollard and Moriarty 1991). Previous studies have shown an increase in sulphate reduction rates (SRR) within seagrass-vegetated sediment and on the below-ground tissue surface of seagrass during photosynthesis, and such stimulation of SRR was attributed to increased

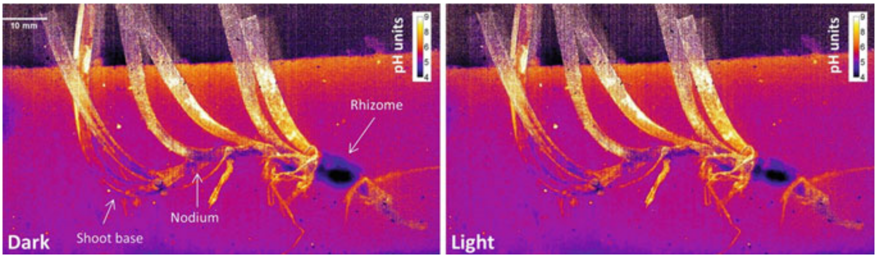

**Fig. 13.12** pH heterogeneity and dynamics in the seagrass rhizosphere determined via novel optical nanoparticle-based pH sensors during a light/dark transition (incident irradiance of 500 µmol photons $m^{-2}$ $s^{-1}$). Colour coded pH image; Legend depicts the pH units. *Left panel* represents measurements in darkness; *right panel* represents measurements in light. The colour coded pH images are the average of three measurements. Data modified from Brodersen et al. (2016). Copyright 2015 John Wiley & Sons Ltd.

exudation of carbohydrates and amino acids (Isaksen and Finster 1996; Moriarty et al. 1986; Blaabjerg et al. 1998; Hansen et al. 2000; Nielsen et al. 2001). The dissolved organic carbon (DOC) exudation from the seagrass rhizome and roots has been estimated to account for 0.7–18% of the total carbon fixed via photosynthesis (e.g. Wetzel and Penhale 1979; Moriarty et al. 1986; Blaabjerg et al. 1998; Hansen et al. 2000).

The chemical speciation of sulphide is pH-dependent, where $H_2S$ predominates at pore-water pH < 7 and $HS^-$ ions at pH > 7. A plant-induced increase in rhizosphere pH can thus shift the chemical speciation towards the non-tissue-permeable $HS^-$ ion, thereby reducing $H_2S$ exposure of the below-ground tissues (Brodersen et al. 2015b, 2016). Brodersen and co-workers (2015b, 2016) showed that regions of the rhizosphere with low pH (down to pH 4) correlated with the presence of plant-mediated oxic microniches (Figs. 13.11 and 13.12), while the tissue surface pH generally was higher than in the bulk sediment. A pH drop within the oxic microshield of the rhizosphere, as a result of the formation of sulphuric acid (i.e. $2O_2 + H_2S \rightarrow 2H^+ + SO_4^{2-}$), can lead to dissolution of carbonates and a concomitant release of sediment-bound phosphorus (Brodersen et al. 2017a; Fourqurean and Zieman 2002; Holmer et al. 2006; Lambers et al. 2009), which then become available for plant assimilation.

An overview of the effect of plant activity on the rhizosphere pH microenvironment at plant/sediment- and oxic/anoxic interfaces is given in Fig. 13.13. Close to selected root/shoot junctions (Fig. 13.13c, e) either a pronounced decrease in pH towards the tissue surface was observed (Fig. 13.13e) indicating chemical re-oxidation of $H_2S$ via ROL and thereby sediment detoxification in these regions, or an increase in pH towards the approximate oxic/anoxic interface was observed, followed by a rapid decrease in pH towards and on the below-ground tissue surface (Fig. 13.13c). The latter is indicative of proton consuming processes, such as

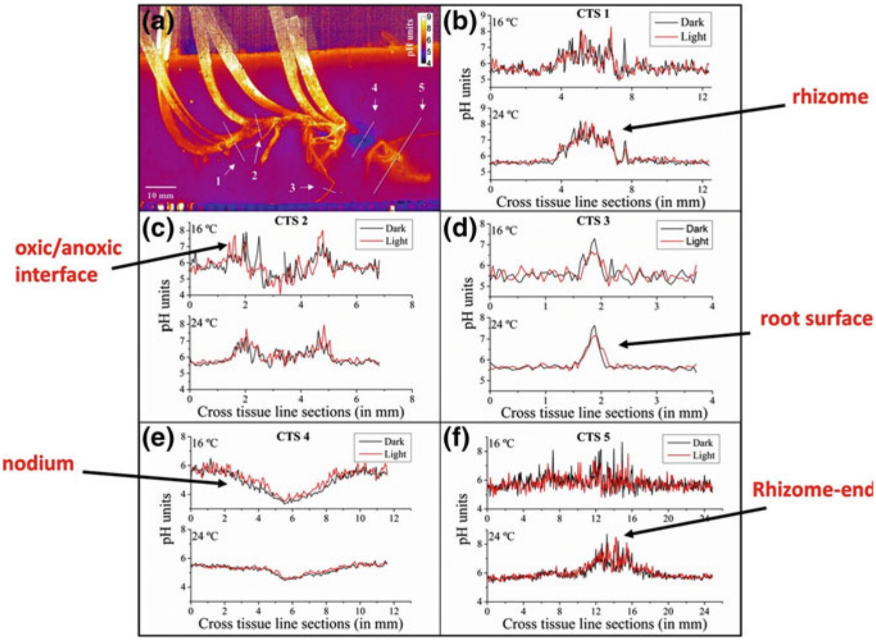

**Fig. 13.13** pH microdynamics in the seagrass rhizosphere at plant/sediment- and oxic/anoxic interfaces measured via novel optical nanoparticle-based pH sensors during light/dark transitions and at temperatures of 16 and 24 °C (where 24 °C represents the temperature optimum for oxygenic photosynthesis in *Zostera marina* L.). **a** Colour coded pH image visualising the extracted cross tissue line profiles in the seagrass rhizosphere. **b**–**f** Cross tissue line section 1–5 as shown in panel a, determining pH microdynamics at plant/sediment- and oxic/anoxic interfaces. Data modified from Brodersen et al. (2016). Copyright 2015 John Wiley & Sons Ltd.

sulphate reduction, at the oxic/anoxic interface followed by chemical re-oxidation of $H_2S$ at the plant/sediment interface (Brodersen et al. 2016). High sediment SRR may lead to a sulphide-induced release of sediment-bound phosphor, from the reduction of Fe(III)oxyhydroxides to Fe(II), as this results in the release of previously sequestered phosphate into the surrounding pore-water (Brodersen et al. 2017a; Pollard and Moriarty 1991; Pagès et al. 2011, 2012). It is therefore intriguing to speculate that a mutual beneficial relationship may exist between the plant hosts and sulphate reducing bacteria based on a reciprocal exchange of nutrients.

Thus there is first experimental evidence that seagrasses can modulate their rhizosphere pH microenvironment. Such changes in pH potentially present an important additional chemical defence mechanism, whereby seagrass plants can further alleviate $H_2S$ toxicity by shifting the sulphide speciation towards non-tissue-permeable $HS^-$ ions.

## 13.4 Effects of Anthropogenic Impacts on Seagrass Habitats and the Rhizosphere Microenvironment

Human activity in coastal marine areas such as boating activities, coastal and harbour development, dredging-induced sediment re-suspension and nutrient loadings, can have profound and adverse effects on the health of adjacent seagrass meadows (Brodersen et al. 2017b; Erftemeijer and Lewis 2006; Orth et al. 2006; Waycott et al. 2009). In fact, seagrass meadows are declining worldwide at an alarming rate (Waycott et al. 2009). This is often a result of synergetic negative impacts on the surrounding environment and thereby seagrass fitness, such as (i) lower light availabilities in the water-column caused by, for example, nutrient-driven algal blooms and/or increased water turbidity from anthropogenic-induced land run-off, adversely regulating rates of leaf photosynthesis during day-time (e.g. Dennison 1987; Short and Burdick 1995; Erftemeijer and Lewis 2006), (ii) enhanced water-column respiration rates during night-time, reducing the water-column $O_2$ conditions and thus the passive $O_2$ influx into the aerenchyma (e.g. Borum et al. 2006), (iii) impeded gas exchange with the surrounding water owing to, for example, nutrient-driven enhanced leaf epiphyte growth further reducing the passive, diffusive $O_2$ exchange and the $CO_2$ uptake of the leaves, thereby potentially leading to inadequate internal aeration and photorespiration (e.g. Maberly 2014; Brodersen et al. 2015a), as well as (iv) high sediment $H_2S$ concentrations, as a response to high sediment SRR fuelled by nutrient inputs, leading to enhanced rhizosphere $O_2$ demands and sediment toxicity (Borum et al. 2005). Enhanced seagrass mortality has thus often been linked to low light availability (e.g. Kim et al. 2015; York et al. 2015) and low night-time water-column $O_2$ conditions (Greve et al. 2003; Pedersen et al. 2004; Borum et al. 2005; Brodersen et al. 2015b) coupled with high sediment $O_2$ demands and $H_2S$ production/concentrations (e.g. Carlson et al. 1994; Borum et al. 2005). These factors can strongly reduce the intra-plant $O_2$ status owing to a reduction in the $O_2$ source and/or an increase in the $O_2$ sink, as the plant-derived rhizosphere oxic microshields, described above, generally ensures protection against phytotoxic $H_2S$ intrusion (Brodersen et al. 2015b). These effects highlight the importance of minimizing environmental disturbance activities in close proximity to seagrass meadows, and pose a challenge for making the increasing exploration of natural resources, e.g. causing increased harbour developments in Australia, environmentally sustainable.

## 13.5 Conclusions

The aerenchyma system of seagrasses ensures aeration of the shoots, rhizomes, roots and, in many cases, the rhizosphere. The shoot and shoot-base manifold are important components of this aeration system and have to be understood to fully understand the aeration of the roots and rhizomes. In particular, the shoot-base manifold seems to ensure that $O_2$ is supplied to the young leaf meristem, and this may be particularly important when $H_2S$ penetrates the roots and rhizomes. However, perhaps the major conclusion in this chapter is that seagrasses can actively alter their rhizosphere microenvironment via release of $O_2$ and allelochemicals into the sediment surrounding their below-ground tissue. This exudation provides a chemical defence mechanism, whereby seagrasses can detoxify their immediate rhizosphere through (i) chemical oxidation of sediment-derived $H_2S$ via plant-released $O_2$, or (ii) shifting the chemical sulphide speciation towards non-tissue-permeable and thus non-phytotoxic $HS^-$ ions by local increase of the rhizosphere pH (Fig. 13.14). Radial $O_2$ loss mainly occurs at the meristematic regions of the rhizome and roots forming oxygenated microzones around the most essential and vulnerable parts of the plants in the otherwise reduced, anoxic sediment environment. The capacity of seagrass below-ground tissue to oxidize the rhizosphere is predominantly regulated by light availability during day-time and by water-column $O_2$ levels during night-time. Overnight water-column hypoxia may lead to inadequate internal aeration of the seagrass, which in turn may result in

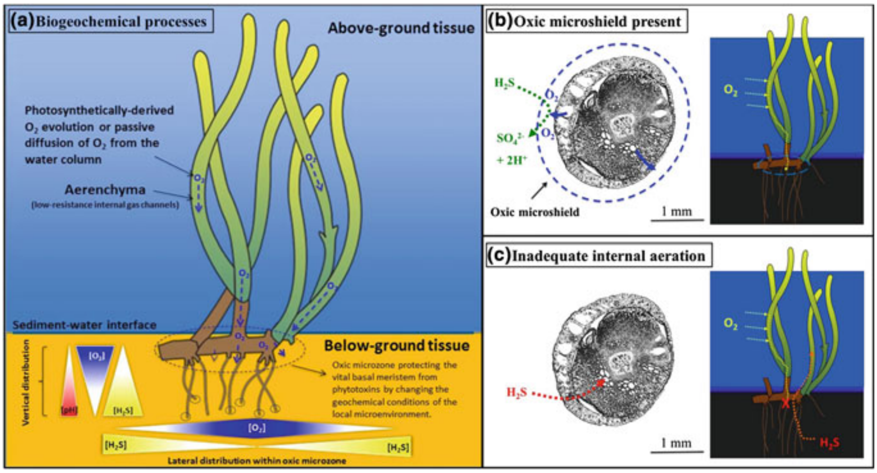

**Fig. 13.14** Conceptual diagram visualising seagrass-derived sediment detoxification. **a** $O_2$ transported down to the below-ground tissue via the aerenchyma is released from the meristematic region of the rhizome (basal leaf meristem), the rhizome and from root apical meristems into the immediate rhizosphere. Radial $O_2$ loss from the below-ground tissue maintaining protective oxic microniches in the immediate rhizosphere, and plant-derived sediment pH changes, chemically detoxifies the surrounding sediment by re-oxidizing sediment-produced $H_2S$ and shifting the geochemical sulphide speciation towards non-tissue-permeable $HS^-$ ions, respectively. **b** Oxic microshield protecting the vulnerable basal leaf meristem. $O_2$ released from the below-ground tissue drives chemical re-oxidation of sediment-produced $H_2S$ within the oxic microniches. **c** Inadequate internal aeration may lead to $H_2S$ intrusion which in turn may kill the plants as a result of chemical asphyxiation. Data modified from Brodersen et al. (2015b). Copyright 2015 John Wiley & Sons Ltd.

sulphide intrusion and thereby increased seagrass mortality owing to chemical asphyxiation. Seagrass plants are thus most vulnerable to phytotoxin intrusion at night-time, where $O_2$ supply to the below-ground tissue to sustain aerobic metabolism and maintain protective oxic microniches in the immediate rhizosphere is completely dependent on passive diffusion of $O_2$ from the surrounding water-column into the aerenchymal tissue of the leaves. The most important structural adaptation of seagrasses to life in sulphidic sediment habitats is therefore, most likely, the formation of suberin tissue barriers to ROL, where the low cross tissue gas permeability ensures efficient transport of $O_2$ to distal parts of the plants and at the same time impedes $H_2S$ intrusion.

Plant-mediated low pH hotspots in the rhizosphere may lead to a concomitant release of sediment-bound phosphorus, which is often the limiting nutrient in carbonate-rich sediments. Modification of rhizosphere pH may thus be important for nutrient mobilization allowing seagrasses to grow in nutrient-limited marine environments. The relatively higher pH levels on below-ground tissue surfaces also indicate secretion of allelochemicals and/or plant-derived stimulation of proton consuming microbial metabolisms, such as sulphate reduction. However, such mechanisms remain speculative and call for direct experimental confirmation.

The chemical defence systems of seagrasses, described in this chapter, are of great importance for the plants. They ensure protection against sediment-produced phytotoxins and provide oxygenated microniches for the growing seagrass roots. Overnight water-column hypoxia and DBL-impeded $O_2$ transport/evolution in the leaves may result in the degradation of the below-ground oxic microshields and $H_2S$ exposure of the below-ground tissue surface. Anthropogenic-induced environmental disturbances causing $O_2$ depletion in coastal marine environments thus represents a major threat to seagrass meadows, as low intra-plant $O_2$ conditions during night-time is a key factor causing events of seagrass die-backs.

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# Chapter 14

# Seagrasses in the South-East Australian Region—Distribution, Metabolism, and Morphology in Response to Hydrodynamic, Substrate, and Water Quality Stressors

**Angus J. P. Ferguson, Peter R. Scanes, Jaimie D. Potts, Matthew P. Adams and Katherine R. O'Brien**

**Abstract** This chapter describes the distribution of key seagrass species in the estuarine-nearshore coastal (ENC) continuum of the south-east region of Australia. We explore the potential influences of hydrodynamics (e.g. tidal currents, wave energy), estuary entrance dynamics (recruitment) and water quality, in addition to light, as primary stressors on seagrass processes and resilience. Despite primary controls exerted by light over seagrass distribution, there are significant areas of euphotic sediments in south-east region that are not colonised by seagrasses. In addition, seagrasses commonly display high degrees of inter-annual variability in coverage which cannot be explained solely by variations in light. We describe the main ecosystem types within the region, and demonstrate how the temporal and spatial gradients in hydrodynamic and water quality stressors (hence light climate), and the availability of suitable substrates for seagrass are controlled by the physical setting or geomorphology of the ecosystem. The opportunistic species *Zostera muelleri* is the most abundant species within the region, primarily occupying the highly dynamic estuarine niche. We provide a focus on *Zostera muelleri* to illus-

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trate the direct positive/negative impacts of hydrodynamic, water quality and estuary entrance morphology stressors on seagrass metabolism and morphology across light gradients.

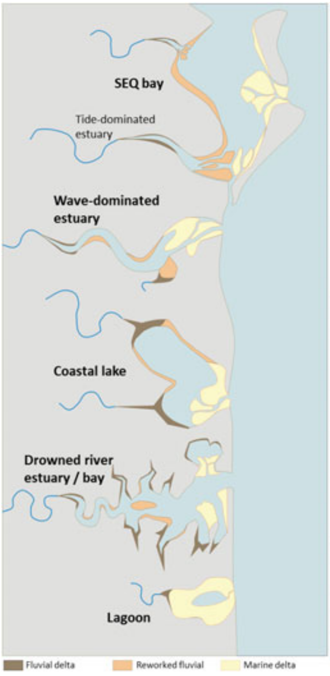
## 14.1 Introduction

Seagrasses are a major biotope of the estuarine and nearshore coastal (ENC) zone of Australia. The ENC zone constitutes a highly dynamic physical and biogeochemical environment, impacted by a wide range of physical stressors (waves, tides, freshwater flows), and physico-chemical water quality stressors, all of which can vary over short (minutes) to long (inter-decadal) timescales. This variation poses large challenges for seagrasses, and has resulted in the evolution of a distinct distribution of species across the ENC gradient. The Australian ENC zone has been broadly divided according to tropical north, south-west and south-east regions, each with its own unique set of dominant stressors determined by climate, geomorphology, and the presence of barrier reefs (Kilminster et al. 2015). Seagrass processes and distribution within the tropical north and south west regions have been comprehensively described previously (Carruthers et al. 2002, 2007), however the south-east region remains poorly described. In this chapter, we provide an overview of the different ecosystem types supporting seagrass in the ENC zone of the south-east region, with a focus on the interactions between seagrass processes and stressors.

Light is recognised as the primary control over seagrass distribution in many systems (Dennison and Alberte 1985; Dennison 1987), and accordingly many seagrass models are based on the prediction of light climate (Gallegos 1994; Cerco and Moore 2001). However a cursory inspection of seagrass distribution patterns clearly shows that many euphotic environments within the ENC zone are not colonised by seagrass, meaning that models based on light alone are insufficient to describe the controls over seagrass distribution. It is increasingly recognised that hydrodynamic stressors such as tidal currents and wave energy can limit seagrass colonisation in shallow environments (Chambers 1987; Fonseca and Bell 1998), while substrate quality can significantly affect the minimum light requirements of seagrass at their lower depth limit (Krause-Jensen et al. 2011; Kenworthy et al. 2014; Ferguson et al. 2016). Physico-chemical water quality may have direct physiological impacts on seagrass health (Enríquez and Rodríguez-Román 2006), while the form and concentrations of nutrients in the water column control the supply of nutrients to seagrasses (Udy and Dennison 1996). Clearly, an understanding of the controls over seagrass metabolism and distribution must also take into account these hydrodynamic, substrate, and water quality stressors, as well as the multiple interactions between stressors.

The temporal and spatial gradients in hydrodynamic and water quality stressors (hence light climate), and the availability of suitable substrates for seagrass are initially dependant on the physical setting or geomorphology of the ecosystem.

Seagrasses are largely confined to estuarine and embayment settings within the south-east region (Kilminster et al. 2015), however these settings comprise distinct system types whose morphology exerts strong controls over stressor gradients. We propose that the species of seagrass observed in the south-east region reflects the nature of variability in hydrodynamics and water quality within these systems, which in turn is driven by the geomorphology of the system (Fig. 14.1). Coastal embayments represent one extreme, where strong connections to marine systems moderate environmental variables such as salinity, temperature and DO, and seagrass communities include significant stands of persistent (Kilminster et al. 2015) species with narrow tolerance ranges for environmental variables, such as *Posidonia australis*. At the other end of the spectrum, intermittent connectivity to the ocean drives large variability in salinity, temperature and DO within coastal lagoons, and seagrass communities are dominated by colonizing species such as *Ruppia megacarpa* or *Halophila* spp. Intermittent entrances can also hinder potential for recolonization after catastrophic events. Wave-dominated estuaries and coastal lakes lie between these two extremes, forming a gradient of environmental conditions, and thus are typically characterized by opportunistic species such as *Zostera muelleri* which has high phenotypic plasticity, and thus capacity to adapt to a gradient/range of environmental conditions.



| Tidal influence | Freshwater flows | Salinity | Wave energy | Nutrients | Seagrass |
|---|---|---|---|---|---|
| **High**<br>- Tidal currents limit seagrass adjacent to channels | Episodic brackish plumes during floods | Oceanic salinity | **High**<br>- Extensive fetch due to open planform | **Low**<br>Particulate and dissolved organic forms only | *Zostera*<br>*Halophila*<br>*Cymodocea*<br>*Halodule*<br>*Syringodium* |
| **Moderate**<br>- Tides Attenuated moving upstream | Floods flush estuary to entrance. | Strong salinity gradient along estuary | **Low**<br>- channelised planform limits wind waves | **Moderate**<br>Particulate and dissolved organic forms only except during floods | *Zostera*<br>*Halophila* |
| **Low**<br>- Tides attenuated greatly across entrance shoals | Episodic brackish plumes during floods. Localised groundwater inputs | Euhaline | **Moderate**<br>- Wind waves cause high bed stress at upper depth limit | **Low**<br>Particulate and dissolved organic forms only | *Posidonia*<br>*Zostera*<br>*Halophila*<br>*Ruppia* |
| **High**<br>- Minimal tidal attenuation at entrance | Episodic brackish plumes during floods | Euhaline | **Low**<br>- High relief catchment topography + channelised planform limits fetch | **Moderate**<br>Particulate and dissolved organic forms only except during floods | *Posidonia*<br>*Zostera*<br>*Halophila* |
| **Low**<br>- Tides only affect system while entrance is open | Dominated by groundwater. Ephemeral overland runoff | Highly variable with periods of hypersalinity | **Low**<br>- Generally small waterway size limits fetch | **Moderate**<br>Dissolved inorganic and organic forms high N:P | *Ruppia* |

**Fig. 14.1** Major system types represented within the ENC of the south-east Australian region

Linkages between seagrass metabolism (productivity and respiration), morphology, and habitat quality (as determined by interactions between key stressors) are fundamental drivers of distribution limits and temporal variability in distribution (de Boer 2007). Broadly, we hypothesise that suitable habitat for seagrasses is determined by:

(1) a stable and biogeochemically tolerable substrate
(2) sufficient light
(3) adequate (but not excess) nutrient supply

In order to recruit and establish viable meadows on a suitable substrate, seagrasses must maintain a tolerable carbon and oxygen balance both internally and at a community scale, and satisfy their nutrient requirements for growth. Where optimal conditions exist for fulfilling these requirements, seagrass can form enduring meadows that are stable over inter-annual timescales. In the concluding section of this chapter, we provide a particular focus on *Z. muelleri* to illustrate the role of interactions between light climate, substrate, hydrodynamics and water quality in the control over seagrass metabolism and distribution. *Z. muelleri* is the primary seagrass species occupying the estuarine niche of the ENC zone. *Z. muelleri* is regarded as an opportunistic species (Kilminster et al. 2015) that has developed a range of strategies to allow it to persist in the highly dynamic estuarine environment. These include:

(1) fast recovery rates via sexual and asexual reproduction
(2) morphological and physiological plasticity in response to variable environmental stressors
(3) ability to tolerate relatively high sulphide stress associated with fine, OM-rich sediments

## 14.2 Ecosystem Types in the ENC

*This section describes the different sub-systems within the ENC zone that support seagrasses, outlining the spatial and temporal dynamics of the hydrodynamic, substrate and water quality stressors.*

There are numerous ecosystem types within the south-east region that support seagrasses, each with its own set of hydrodynamic, substrate, and water quality stressors that control the distribution of seagrasses (Fig. 14.1). Across the latitudinal gradient, there is gradient of higher diversity at the northern limit of the region due to the presence of numerous tropical opportunistic species, while the persistent species *Posidonia australis* reaches its northern limit of distribution at Wallis Lake on the NSW central coast. Within the region, the systems dominated by oceanic water quality tend to have the greatest diversity of seagrass species, while estuarine systems dominated by variable brackish conditions but still open to tidal exchange

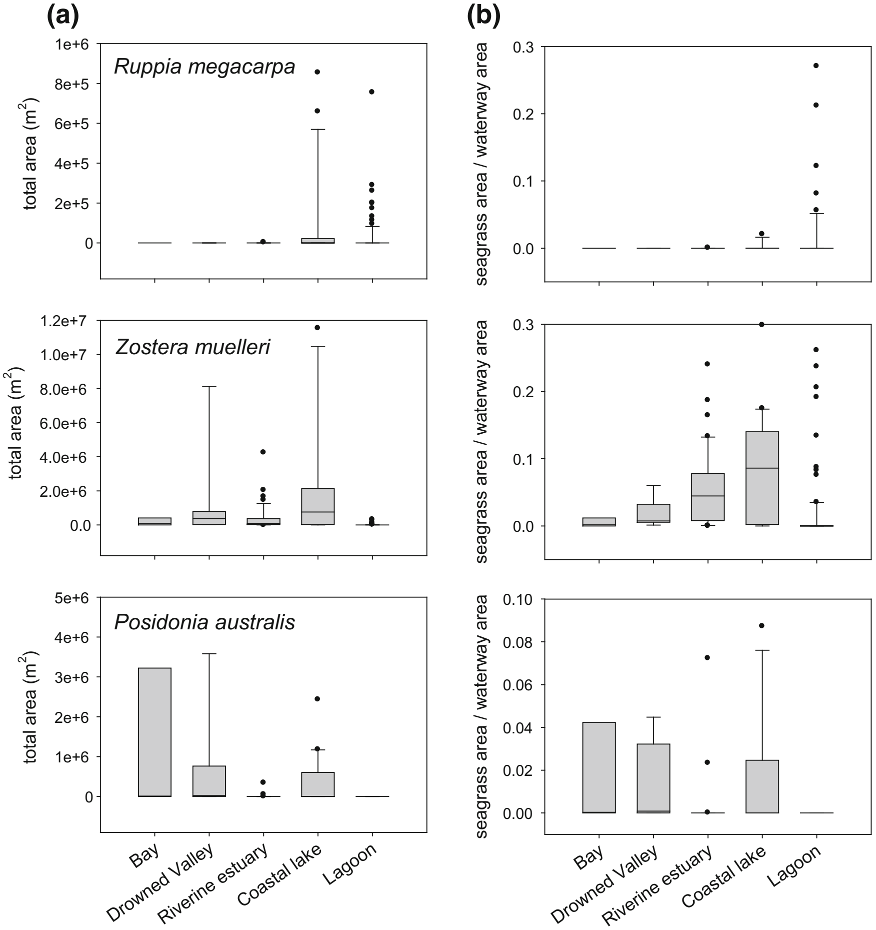


**Fig. 14.2** The distribution of main seagrass species across system types along the NSW coast: **a** total area, and **b** seagrass area/waterway area

are dominated by the opportunistic *Z. muelleri*. Systems more isolated from marine exchange tend to become more dominated by Ruppia (Fig. 14.2). This gradient of seagrass species distribution provides the rationale for much of the subsequent analysis within this chapter. We characterise the environmental stressors associated with seagrass presence/absence, and provide particular focus on the conditions associated with *Z. muelleri*.

## 14.2.1 Geomorphic Classifications

An estuarine classification scheme incorporating the concept of morphological maturity developed by Roy et al. (1980) is a useful framework for understanding the distribution and dynamics of environmental stressors for seagrass within the ENC zone. In general, freshwater flows from overland runoff deliver sediments that are deposited across estuarine gradients: coarser sediments forming fluvial deltas within the upper estuarine reaches, and finer sediments being deposited in the central mud basin. At the oceanic end, wave energy causes the formation of entrance barriers while tidal flows cause the formation of marine sand deltas within entrance channels. Over geological timescales, the progradation of fluvial deltas and infilling of central mud basins causes a reduction in waterways area and a more channelized estuary form (Roy et al. 1980, 2001; Heap et al. 2004).

Below we present an overview of the morphology and evolutionary stage of the key ecosystem types supporting seagrass in ENC zone, highlighting the implications of system morphology for environmental stressor gradients (see also Fig. 14.1).

### 14.2.1.1 South East Queensland Marine Embayments

In south east Queensland, extensive marine embayments protected from ocean wave energy are formed by the presence of large sand islands (e.g. Moreton Bay and the Great Sandy Straits). These systems have morphological similarities to immature coastal lakes of the central NSW coastline, however ocean exchange is much greater. Freshwater inputs to SEQ marine embayments occur via generally turbid tide-dominated estuaries, which form reworked fluvial sediment deltas in the western bays (Heap et al. 2004). Large marine delta shoals form at the ocean passages, with large tidal currents associated with main channels. Seagrasses are dominated by *Z. muelleri* and *Halophila* in the western fluvial delta shoals, giving way to much greater diversity of tropical and temperate opportunistic species in the more sheltered areas of the eastern marine delta shoals (Roelfsema et al. 2009, Roelfsema 2014).

### 14.2.1.2 Mature Tide-Dominate Riverine Estuaries

Tide-dominated riverine estuaries are the predominant estuary type along regions of the Queensland coast protected from ocean wave energy by either large islands or the GBR. Most are morphologically mature, with absence of wave-formed barrier at the entrance resulting in a funnel-shaped planform. This results in amplification of tidal currents within the middle to upper reaches of the estuary causing high rates of sediment resuspension and associated turbidity. Hydrodynamic stresses and light-limitation associated with turbidity are major limitations to seagrass within the estuary. Seagrasses are dominated by *Z. muelleri* and *Halophila*, being largely confined to shoals at the estuary entrance and within the adjacent coastal waters.

#### 14.2.1.3 Mature Wave-Dominated (Barrier) Riverine Estuaries

Wave-dominated, riverine (barrier) estuaries are well represented along the exposed coast of central to northern NSW, (Roy et al. 2001; Fig. 14.2). In their mature state, the central mud basin has largely been infilled resulting in a channelised planform that is in equilibrium with tidal and freshwater flows. Many systems also include tributaries that are morphologically less mature (known as 'broadwaters') and are actively infilling with catchment derived sediment. Tidal currents are greatest at the entrance ($\sim 1$ m $s^{-1}$) and are moderately attenuated moving upstream. Wind wave energy is limited by fetch due to the channelised planform of the estuary. Seagrasses in these systems are dominated by *Z. muelleri* and are generally confined to cut-off channels and embayments of the lower estuarine reaches, with the upstream limit of distribution most likely controlled by water quality and sediment quality gradients.

#### 14.2.1.4 Immature Wave-Dominated Coastal Lakes

Wave-dominated coastal lakes are a prominent system type of the central to southern NSW coastline, representing a morphologically less mature form of riverine (barrier) rivers. They generally include an extensive central mud basin with small fluvial deltas associated with freshwater inputs, and extensive marine deltas. The smaller freshwater inflows relative to waterway area result in generally less efficient ocean entrances, which may become further constricted or periodically close during extended dry periods. Tidal currents are greatly attenuated upstream of the entrance due to frictional effects across marine delta shoals, resulting in a generally micro-tidal regime within lake basins. The planform and morphology of coastal lakes is highly variable across NSW, ranging from deep systems resembling drowned river valleys (e.g. Lake Macquarie), shallow open basins (e.g. Tuggerah Lakes), elongate systems (e.g. Lake Tabourie), and complex hybrid systems (e.g. Wallis Lake). Coastal lakes support the largest area of seagrasses within the NSW part of the south-east region (Fig. 14.3), with up to 30% of the area of some waterways occupied by seagrass. Distributions are characterised by *Z. muelleri* and *Halophila ovalis* on fluvial delta and reworked shoals, and a mix of *Z. muelleri* and *P. australis* on the more sheltered marine delta shoals.

#### 14.2.1.5 NSW Marine Embayments and Drowned River Estuaries

NSW marine embayments are predominantly associated with the lower reaches of drowned river valley estuaries and are a prominent feature of the Hawkesbury Shelf

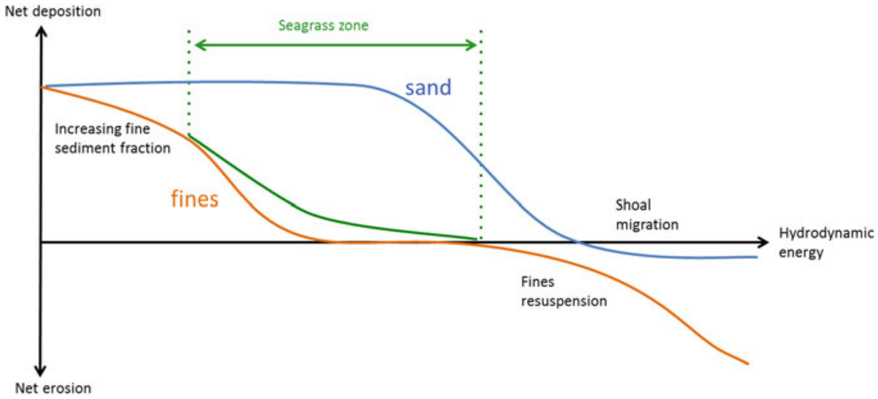


**Fig. 14.3** Model of the interactions between hydrodynamic energy and the stability of seagrass substrates. The balance between net deposition/erosion of fine sediment and sand fractions (*y* axis) varies as a function of hydrodynamic energy (*x* axis). Substrate quality (i.e. the relative proportions of fine and sand fractions) can be implied by the interaction of this scale and TSS concentrations. In very low hydrodynamic energy environments with high TSS concentrations, the settling of fines will result in muddy substrates unsuitable for seagrass colonisation. In high hydrodynamic energy environments, sand substrates become unstable and shoal migration occurs. A theoretical optimum zone for seagrass colonisation exists where shoals are stable but not overly enriched with fines. The presence of seagrass meadows within this zone causes a reduction in near bed velocities thereby enhancing the tendency for net deposition (as indicated by the green curve)

region. These systems are characterised by deep central basins flanked by narrow reworked fluvial shoals and fluvial delta associated with smaller tributaries. The presence of marine delta shoals is variable, being largely absent in deeper systems but extensive in more shallow systems such as Port Stephens and Botany Bay. NSW marine embayments support the largest area of *P. australis* within the south-east region, with significant areas of *Z. muelleri* in some systems.

#### 14.2.1.6 Coastal Lagoons

Coastal lagoons are common along the NSW coastline, existing in the smaller coastal catchments with ephemeral overland freshwater flows. There is mounting evidence that submarine groundwater discharges from surrounding swamps and barrier dunes contribute the main freshwater delivery pathway to these systems. Due to the low overall freshwater discharges, lagoon entrances predominantly remain closed, opening only during rainfall/runoff events large enough to cause overtopping of the entrance berm. Entrance closure time is determined by the degree of channel scour during opening, and the prevailing wave climate and sand supply along the adjacent coastline which affects the formation rate of the entrance berm. Seagrass diversity in these systems is related to the entrance opening frequency, with predominantly closed systems (i.e. ‘back dune lagoons’) being exclusively colonised by *Ruppia*, and more frequently opened systems colonised by a variable mix of *Z. muelleri* and *Ruppia*. Intermittent entrances also make lagoons susceptible to catastrophic events such as the occurrence of extreme environmental conditions occurring during the millennial drought experienced by ENC in 2008–2010, and can inhibit recolonization after catastrophic events (e.g. Durras Lake in NSW lost all of its extensive *Z. muelleri* beds in 2009–2010 and recolonization did not re-occur until 2015) (P. Scanes, personal observations).

## 14.3 Environmental Stressors in the ENC Zone

*This section reviews the gradients and interactions between hydrodynamics, substrate quality, and water quality as drivers of seagrass processes.*

### *14.3.1 Hydrodynamics*

Hydrodynamics is defined as encompassing a range of physical processes including:

- Freshwater flows
- Tidal currents
- Wind driven currents
- Turbulence due to orbital wave velocities

These physical processes have profound impacts on substrate stability and quality for seagrasses, and on water quality stressors. There are clear linkages and feedbacks between system morphology and the relative importance of different hydrodynamic stressors in determining seagrass distributions. Due to the skewing of seagrass communities towards the marine influenced regions of estuaries and lakes, freshwater flows only directly impact seagrasses for relatively short periods of time during flood events. However, the magnitude of freshwater flows (which is in part driven by catchment size) is a primary determinant of the geomorphic maturity, and hence planform, of the system, as well entrance conditions and tidal influence (Roy et al. 2001). Many of the hydrodynamic stressors discussed in this section are directly influenced by the overarching effects of freshwater flows.

#### 14.3.1.1 Timescales of Hydrodynamic Influences

Over long timescales (decades to centuries) hydrodynamic forces shape the distribution of sediment facies (e.g. grain size and organic matter [OM] content) within each of the system types shown in Fig. 14.3. This sets broad limits to the distribution of suitable substrate types available for seagrass colonisation within the south-east region. Anthropogenic disturbances (e.g. increased total suspended solids (TSS) loads due to catchment clearing, alterations to tidal regimes due to dredging and entrance training works, increases in OM supply due to eutrophication) have altered sediment facies distribution with flow-on impacts on seagrass distribution (Harris 2001).

Over shorter timescales, hydrodynamic forces such as freshwater flows and tidal currents influence the stability of substrates. There is a clear gradient of diminishing freshwater inflows and tidal ranges across the seagrass presence/absence gradient within NSW systems. This co-variation between these stressors reflects the tendency for higher freshwater inflows in larger systems to maintain an open entrance and hence tidal influence. Tidal range is also significantly influenced by attenuation across the entrance shoals, which in coastal lakes can result in micro-tidal ranges throughout much of the lake basin.

#### 14.3.1.2 Shoal Migration

Extensive euphotic shoals exist in the lower estuaries and coastal embayments of the ENC zone (Fig. 14.1), however establishment of enduring seagrass meadows is limited by the rate of shoal migration due to wave energy and tidal currents relative to the recruitment and growth of seagrass (de Boer 2007). In more channelised riverine estuaries such as the Tweed estuary, tidal currents result in constant shoal migration in the active marine delta that largely precludes seagrass colonisation, despite favourable light and nutrient supply conditions (Figs. 14.4 and 14.5). Accordingly, seagrass meadows are restricted to sheltered cut-off channels and embayments of the lower estuary. Similar limitation of seagrass colonisation occurs in the active marine delta regions of the eastern banks in Moreton Bay (Adams et al. 2016b). Within coastal lakes, tidal currents are quickly attenuated across entrance shoals, allowing greater seagrass colonisation of less mobile shoals within the lake basin. The training of lake entrances by the construction of breakwalls maintains a constant connection with the ocean and increases the lake tidal prism resulting in more active entrance shoals and loss of seagrass due to smothering or erosion. This is graphically illustrated by the loss of extensive *Z. muelleri* meadows in Lake Illawarra after entrance training works were completed in 2005 (Fig. 14.4).

#### 14.3.1.3 Wave Energy

Wave energy in shallow systems can cause significant bed shear stress that may preclude seagrass colonisation at the upper limit of its depth range (de Boer 2007; Vacchi et al. 2014). Predictive models of seagrass distribution are greatly improved for shallow depths if wave energy is accounted for (Angus Ferguson, personal observations, (Saunders et al. 2013; Adams et al. 2016c)). For example, in Moreton Bay, seagrass habitat is more likely to occur in regions where the mean significant wave height is less than 0.6 m (Adams et al. 2016c). Wave energy is more likely to

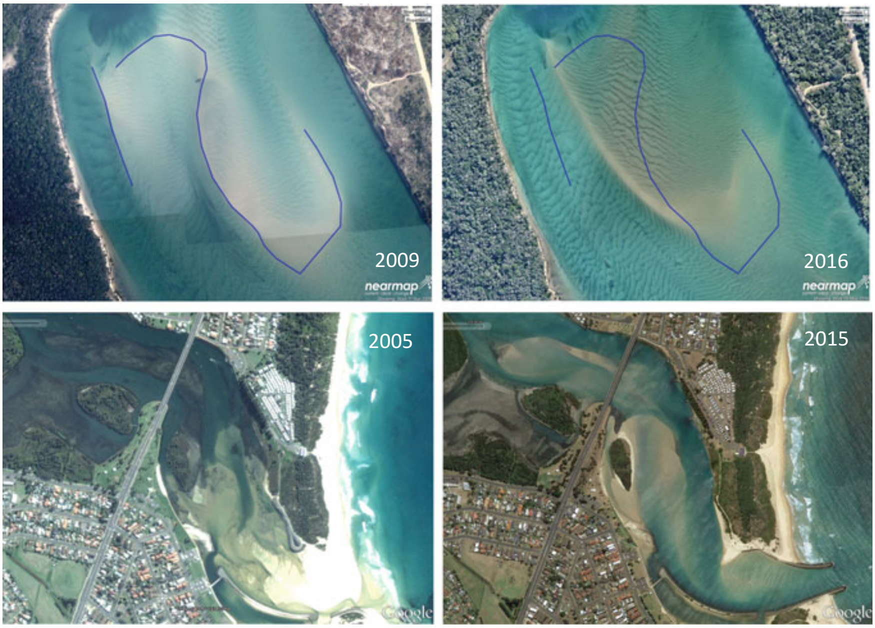


**Fig. 14.4** Top panels: Example of active shoal migration in the lower Tweed estuary, evident from meso-scale ripples and mega ripples. The ridge line of the mega-ripple structure evident in the 2009 image is indicated by the blue line in both images. Bottom panels: The entrance to Lake Illawarra showing the loss of seagrass due to smothering by prograding marine delta shoals induced by an increase in the tidal prism following the construction of entrance training walls

control seagrass distribution in more exposed ENC zone types, where waves can develop over longer fetches (e.g. large lagoons and coastal embayments). Waves can also resuspend sediment (Lawson et al. 2007), reducing water quality and therefore the habitat area where benthic light availability is sufficiently high for seagrass persistence. *Z. muelleri* exhibits low above ground biomass: below ground biomass (AGB:BGB) in environments exposed to high wave energy, suggesting a morphological response to aid in resisting disturbance due to bed shear stress (Ferguson et al. 2016).

#### 14.3.1.4 Sheltering

A dampening of hydrodynamic forces can occur due to physical barriers (e.g. breakwalls) or the effects of seagrass biomass extending to the water surface (Abdelrhman 2003), resulting in relatively quiescent conditions and minimal water exchange. This can have profound implications for water clarity (e.g. negative feedbacks on resuspension), substrate quality (e.g. enhanced trapping of particulates), ambient temperature and dissolved oxygen conditions, and nutrient supply

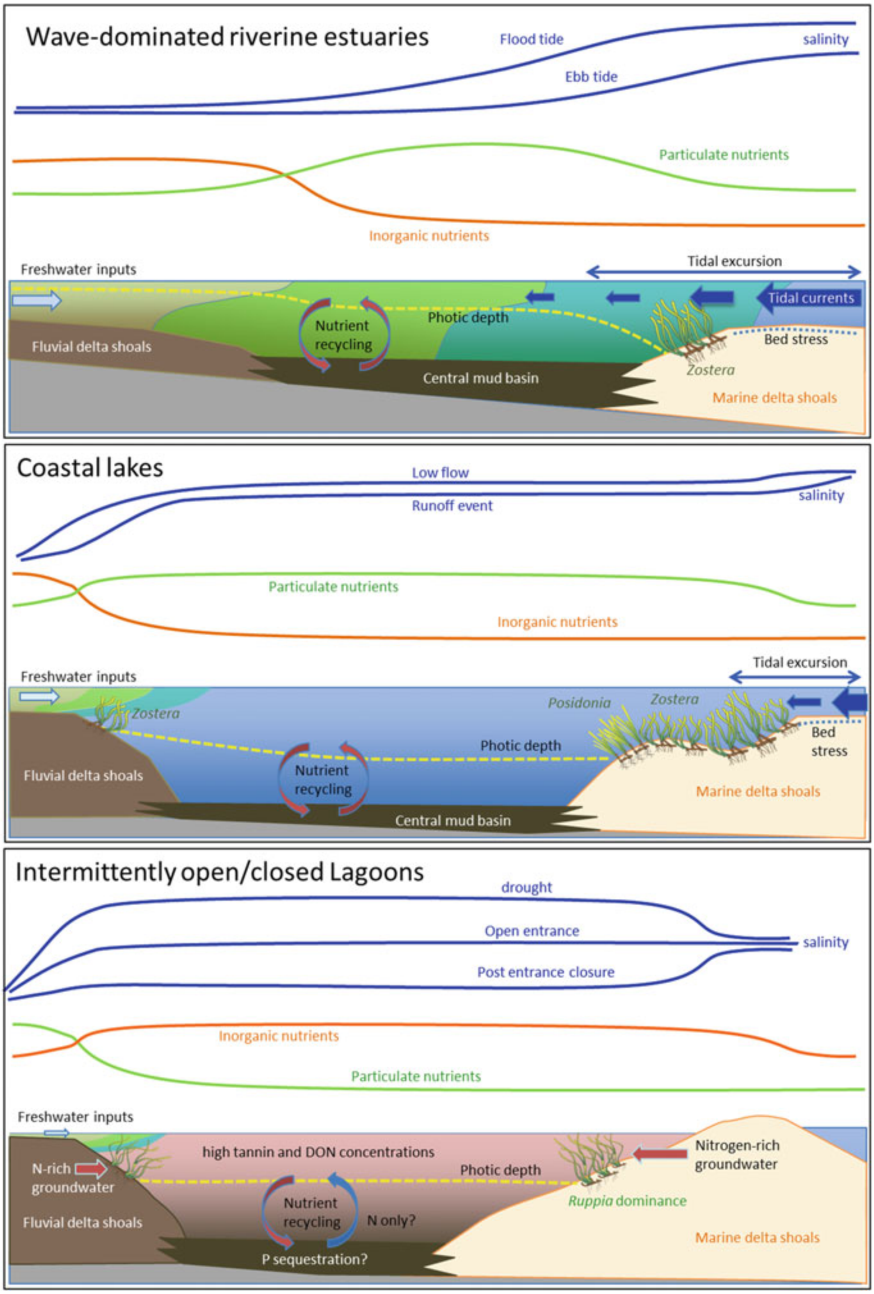


**Fig. 14.5** Primary ecosystem types supporting seagrasses in the ENC zone, showing the main water quality and hydrodynamic stressor gradients that determine suitable habitat. In reality, some systems display aspects of two or more of these generalised models

(Fonseca and Bell 1998; Agawin and Duarte 2002; Binzer et al. 2005). Within Tuggerah Lakes, *Z. muelleri* meadows proliferating in a band approximately 200 m from the shoreline have hydrodynamically decoupled the nearshore zone from the lake basin resulting in distinct water quality and ecological processes. The dampening of water exchange has caused localised eutrophication impacts adjacent to stormwater outlets along the inshore edge of the *Z. muelleri* meadows (Brennan et al. 2011b).

## *14.3.2 Water Quality*

Water quality can impose direct physiological stresses on seagrass when stressor values (e.g. temperature, salinity) are outside of the optimum range for a particular species (Kerr and Strother 1985; Collier et al. 2011, 2014). Similarly, an optimum range for nutrient supply exists: too little and limitation develops, too much and eutrophication and toxicity impacts develop (Lee et al. 2007). The interaction between many aspects of water quality also determines the optical properties of the water column, which in turn controls the light climate of potential seagrass substrates. In this section we review how system morphology influences water quality gradients, and the implications of this for the distribution of seagrass communities.

### 14.3.2.1 Salinity

Spatial and temporal variation in salinity gradients differs markedly between the different ecosystem types within the south-east region (Fig. 14.5). Marine embayments (e.g. Moreton Bay, Port Stephens, Botany Bay, and Jervis Bay), and coastal lakes with efficient ocean entrances (e.g. Wallis Lake) are dominated by oceanic water for the majority of the time, with relatively brief intrusions of brackish surface water plumes associated with flood events. *Posidonia*, *Cymodocea, Syringodium* and *Halodule* are found exclusively in these environments within the south-east region, suggesting either a preference for ocean water salinities or an aversion to hypo-saline conditions. Studies on the effects of hypo-salinity on these species are rare, however it appears that oceanic salinity is optimal for *Halodule* (Collier et al. 2014) and *Cymodocea*, with sub-lethal effects at salinities of about half seawater (Fernandez-Torquemada and Sanchez-Lizaso 2011). In contrast, a study of salinity tolerance in *Posidonia* found no effects on leaf growth at salinities as low as 13 (Tyerman et al. 1984), while the optimal salinity for *Syringodium* has been estimated to be as low as 25 (Lirman and Cropper 2003). The paradox of species with apparent tolerance to hyposalinity being confined to settings dominated by oceanic water has been noted before (Collier et al. 2014), and it has been suggested that it may reflect either (1) the relative short duration of studies, or (2) limitation due to other factors associated with low salinity (e.g. turbidity, high inorganic nutrient concentrations). We suggest an alternative explanation, whereby *Posidonia* is precluded from less stable environments over inter-annual timescales due to slow rates of colonisation.

The optimum salinity for *Zostera* has been estimated to be 36, however it has also been shown to tolerate salinities as low as 3 for more than 10 weeks (Collier et al. 2014). The stress-induced morphometric response to hypo-salinity in this case was a large increase in shoot density. These observations are consistent with the occurrence of *Zostera* across a wide range of salinities (Fig. 14.6), but predominantly in association constant tidal influence. Within larger riverine estuaries such as the Tweed and Richmond Rivers on the NSW north coast, *Zostera* is confined to the marine delta shoals in the lower estuarine reach. These systems are characterised by strong salinity gradients between the freshwater and ocean end members, with minimal vertical stratification occurring outside of high flow events (Eyre and Twigg 1997). The salinity gradient is displaced significantly along the estuary as a function of both tidal excursion and freshwater inflow, and *Zostera* is exposed to a wide range of salinities at hourly to inter-annual timescales. Similar to *Posidonia*, it is unlikely that it is a response to salinity alone determines the upstream limit of *Zostera* distribution in these systems but rather a combination of other factors that co-vary along the salinity gradient. For example, upstream of the marine delta shoals coincides with more polyhaline conditions (18–30) where salinity induced flocculation of suspended sediments and phytoplankton results in much greater fine sediment and organic matter contents of substrates (Hossain et al. 2002). This would increase the minimum light requirements of seagrass in these locations, which in combination with higher turbidity may preclude the establishment of meadows.

*Ruppia* is generally regarded to tolerate a much wider range of salinities than either *Zostera* or *Posidonia,* with a preference for freshwater but an ability to survive salinities up to 75 (Adams and Bate 1994). This is consistent with the observed distribution of *Ruppia* in the south-east region, where it is most prevalent in lagoons. Salinity in lagoons is generally highly variable over longer timescales, with variation occurring primarily as a function of entrance opening/closure frequency and evaporation during periods of entrance closure. During open entrance conditions, freshwater runoff can initially cause a dramatic reduction in salinity followed by a rapid salinity increase as tidal flows penetrate the lagoon. The degree of salinity increase depends on continuing freshwater flows and the duration of entrance opening, with the salinity at the time of closure setting conditions in the lagoon for the subsequent period (Pollard 1994). There are examples of periodic hypersaline conditions occurring in NSW lagoons such as Lake Tilba Tilba and Willinga Lake, all of which are dominated by *Ruppia*. Wide scale mortality of *Z. muelleri* in response to the onset of hypersaline conditions in Durras Lake suggests intolerance to salinities in excess of seawater for long periods (months to years). There are multiple instances of *Ruppia* in association with localised submarine groundwater discharges in larger NSW coastal lakes which is consistent with its demonstrated preference for freshwater (Adams and Bate 1994).

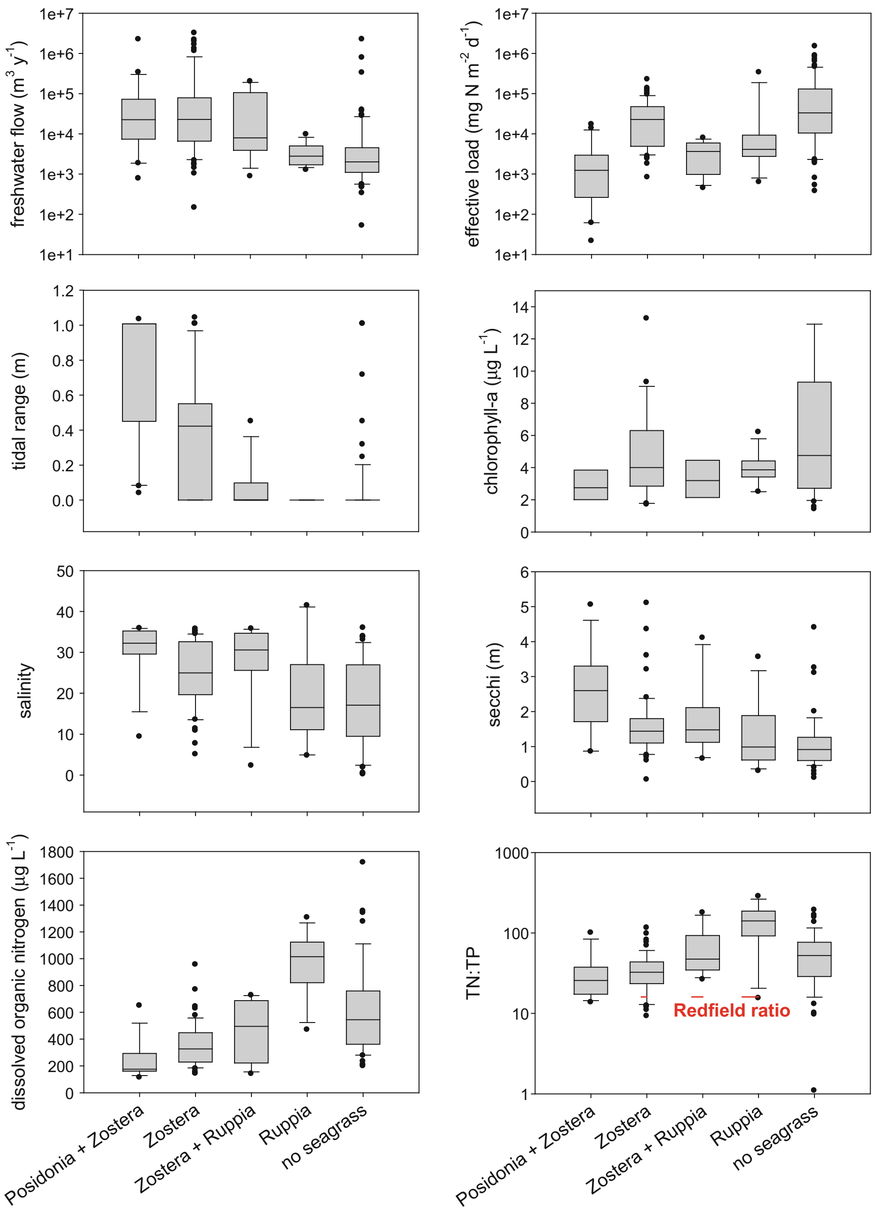


**Fig. 14.6** Boxplots of physical attributes and water quality in systems grouped according to the seagrass species present. Based on an analysis of 184 estuaries within NSW

#### 14.3.2.2 Temperature

With the exception of lagoons, seagrasses in the south-east region occupy systems where temperatures are moderated by oceanic influence. There are no significant differences in mean temperature among system types open to tidal effective exchange (Ferguson unpubl. data), with the annual mean temperature across the region being 24 °C (±5 °C seasonal swing). There is however a significant latitudinal temperature difference of approximately 5 °C between Moreton Bay and the southern border of NSW. The implications of these temperature trends for seagrass metabolism are discussed below.

Seagrass gross primary productivity (GPP) has been shown to peak at an optimum temperature, below and above which the GPP declines (reviewed in Lee et al. 2007). Based on measurements in Moreton Bay and Green Island, seagrass GPP was found to peak at 31 °C for *Zostera muelleri* and 35–36 °C for *Cymodocea serrulata* and *Halodule uninervis*, and this result was found to be independent of latitude (Adams et al. 2017). However, optimum temperatures for NPP are expected to be lower than optimum temperatures for GPP, because seagrass respiration increases with temperature (Pedersen et al. 2016; Collier et al. 2017; Staehr and Borum 2011). Hence, the optimum temperatures for seagrass GPP stated above represent a maximum for these seagrass species. For example, *Zostera muelleri* from Lake Macquarie, NSW, has been shown to reduce above-ground biomass and have smaller leaves at 30 °C than at 27 °C (York et al. 2013), indicating that the optimum temperature for *Zostera muelleri* is less than 30 °C, which is a few degrees lower than the reported optimum temperature for GPP (31 °C, (Adams et al. 2017). This suggests that the south-east region represents the optimum temperature range for *Zostera muelleri*, but is likely below the optimum for other opportunistic species like *Cymodocea serrulata* and *Halodule uninervis.* Chronic exposure to elevated temperatures (5–6 °C above ambient, e.g. near heated effluent outlets) leads to permanent loss of *Zostera muelleri* (York et al. 2013).

The analysis of temperature at the system level does not provide an indication of localised temperature gradients within meadows. Temperatures during the day due to solar heating can exceed ambient temperatures by up to 7 °C at the shallow limit of meadows (Adams et al. 2016a). The continued presence of *Zostera muelleri* at these sites indicates that diel temperature swings in this range are sub-lethal, however metabolic and morphological changes relative to deeper parts of the meadow indicate potential negative impacts due to temperature (Adams et al. 2016a; Ferguson et al. 2017). At higher temperatures, short-term heat stress can irreparably damage the photosynthetic condition of seagrass leaves (Campbell et al. 2006) and lead to complete mortality of seagrass shoots after only a few days (Collier and Waycott 2014). Whilst both short-term and long-term heat stress might appear to be a greater threat to seagrass at tropical latitudes, temperate seagrasses are expected to be similarly vulnerable to climate change-induced heat stress (Jordà et al. 2012). Localised heat stress impacts on seagrass can also be driven directly by anthropogenic stressors; for example, observational evidence has demonstrated the widespread loss of *Z. muelleri* in areas of Lake Macquarie impacted by thermal pollution from power station cooling water (Angus Ferguson, personal observations). Severe heat stress on *Z. muelleri* can occur at 32 °C (York et al. 2013), whilst for other Australian species, temperatures at 40 °C or higher will likely cause significant declines in seagrass habitat (Campbell et al. 2006, Collier and Waycott 2014).

#### 14.3.2.3 Nutrient Concentrations and Quality

*Marine embayments, riverine estuaries and coastal lakes*

Seagrasses are capable of assimilating nutrients from the water column via leaves (Stapel et al. 1996), however most species in the south-east region exist in oligotrophic environments characterised by low ambient concentrations of dissolved inorganic nutrients. It is therefore likely that trapping of particulate organic nutrients (e.g. phytoplankton detritus) and recycling of these nutrients within the rhizosphere constitutes the primary nutrient supply pathway supporting seagrass growth (Gacia et al. 2002). *Z. muelleri* meadows experience large changes in coverage and density over seasonal and inter-annual timescales, and lose up to 45% of GPP as wrack (Ferguson et al. 2017). This implies a reasonably low conservation of nutrient resources within *Z. muelleri* meadows relative to more persistent seagrass species. Nutrient budgets constructed for a *Z. muelleri* meadow in a NSW coastal lake indicate that losses due to export of wrack are closely balanced by inputs due to particulate trapping (Ferguson et al. 2017).

In riverine (wave-dominated) estuaries, inorganic nutrients delivered by freshwater inputs are largely assimilated by phytoplankton in the upper to middle reaches where residence times are greatest (Ferguson et al. 2004), meaning that nutrient supply to seagrass meadows in the lower estuarine reaches is dominated by ebb tide export of particulate and dissolved organic forms (Figs. 14.5 and 14.6). Similarly, inorganic nutrient inputs to coastal lakes are rapidly assimilated by phytoplankton following runoff events, resulting in low ambient concentrations within lake waters. Recycling of nutrients via remineralisation of phytoplankton detritus in aphotic lake basin sediments provides a continuous supply of nutrients supporting subsequent phytoplankton productivity (Brennan et al. 2011a). Seagrass meadows in coastal lakes are therefore exposed to reasonably stable concentrations of particulate and dissolved organic nutrients.

*Coastal lagoons*

Nutrient supply and quality in coastal lagoons is distinctly different to that of other systems within the south-east region (Figs. 14.5 and 14.6). These systems are characterised by extremely high concentrations of dissolved organic nitrogen

(DON), which is the strongest predictor of the seagrass presence/absence gradient within NSW systems (Fig. 14.6, PRIMER-BEST analysis). DON concentrations are negatively correlated with surface freshwater inflows, and there is mounting evidence that this reflects an increase in the relative influence of groundwater inputs in smaller coastal waterways (OEH unpubl data). The exclusive presence of *Ruppia* appears to be strongly associated with DON, and even within systems with mixed assemblages of *Z. muelleri* and *Ruppia*, the location of *Ruppia* meadows is highly correlated with indicators of likely groundwater influence. This result suggests either a preference or greater tolerance by *Ruppia* for groundwater inputs.

The composition of DON is largely uncharacterised for Australian systems, however it likely that the DON pool comprises a wide and variable range of different compounds (Bronk et al. 1994; McCarthy et al. 1997; Burdige and Zheng 1998; Berman and Bronk 2003), each with its own light attenuation, nutrient, and potential allelopathic properties (Babin et al. 2003; Kraus et al. 2003). It has been estimated that up to 40% of the DON pool may be bio-available (Seitzinger and Sanders 1997), and therefore may influence seagrass nutrition. This is supported by a close relationship between DON concentrations and tissue nitrogen contents across the south-east region (Ferguson unpubl. data). There is also a close relationship between DON and coloured dissolved organic matter indicating that high DON concentrations are associated with greater light attenuation. However this effect is regional, with a higher slope for the DON:CDOM relationship in northern NSW systems most likely reflecting an interaction between geological and climate factors (Ferguson unpubl. data).

Another defining feature of nutrient dynamics in coastal lagoons are significantly lower phosphorus concentrations and higher N:P ratios compared to other system types, suggesting potential phosphorus limitation of primary productivity (both phytoplankton and seagrasses) in these systems. The mechanisms responsible for low phosphorus concentrations are unclear, however it is potentially a combination of low phosphorus concentrations in inputs (influenced by catchment geology and the submarine groundwater discharges), and sequestration of phosphorus in lagoon sediments.

#### *High nutrient concentrations*

In general, systems within the south-east region are oligotrophic, therefore instances of potential negative impacts to seagrass due to high nutrient concentrations are rare. A small subset of *Ruppia* dominated lagoons commonly exhibit extremely high ammonium concentrations in excess of 500 $\mu g\ L^{-1}$ which are potentially toxic to seagrass (van Katwiljk et al. 1997). This may explain the absence of *Zostera* from these systems, however other factors such as protracted periods of entrance closure leading to salinity and or temperature extremes and groundwater influence may also be important. The classic eutrophication paradigm describing a loss of seagrass due to increased macroalgae productivity and biomass Collier and Waycott (2009) is only apparent in a small number of systems in the south-east region.

Localised nutrient enrichment of the nearshore zone in Tuggerah Lakes causes a proliferation of macroalgae species that can displace *Zostera* and *Ruppia* (Brennan et al. 2011b). However, higher nutrient availability in this system is also resulting in positive impacts on *Zostera* growth (as suggested by Udy and Dennison 1997), evidenced by extremely high standing stocks of above ground biomass (Ferguson et al. 2016). The seagrass, however, only survives at very shallow depths and probably represents the last step before total loss. Notably, the systems within the region without any seagrass present are characterised by high inorganic nutrient loadings relative to their size combined with predominantly closed entrance conditions, resulting in high phytoplankton biomass (Fig. 14.6). This contrasts with wave-dominated estuaries that have similar loadings, where inorganic nutrient loads are processed within the upper and middle reaches, and exported to the lower estuary and ocean in organic forms.

#### 14.3.2.4 Total Suspended Solids

Total suspended solids (TSS defined here as inorganic fine sediments and organic particulates (allochthonous OM and phytoplankton detritus)) exert primary controls over light climate and substrate quality in seagrass habitats. Gradients in TSS are broadly controlled by interactions between: (1) freshwater inputs, (2) oceanic inputs, (3) in situ production of phytoplankton, and (4) resuspension due to wave energy and tidal currents. In riverine (wave-dominated) estuaries, salinity gradients are the primary control over TSS concentrations. Inorganic TSS concentrations due to freshwater inputs tend to be highest in the upper reaches and diminish towards the middle estuary due to flocculation and settling across the salinity gradient (Eyre 2000). Improvement in light climate within middle estuary reaches promotes phytoplankton productivity and biomass thereby maintaining high overall light attenuation (Ferguson et al. 2004). Further flocculation, coagulation, and settling of TSS within polyhaline reaches (salinity 18–30) causes enrichment of organic matter and fine sediment contents of benthic substrates. These patterns in TSS and their impact on substrate quality serve to limit the upstream extent of seagrass colonisation in wave-dominated estuaries.

In contrast, salinity gradients in coastal lakes are far less pronounced and, outside relatively short-lived flood events, TSS concentrations are dominated by phytoplankton biomass (Roy et al. 2001). In shallow systems (e.g. Tuggerah Lakes), resuspension of bed sediments due to wind waves contributes significantly to TSS causing severe light limitation in the lake basin. The damping of wave energy by seagrass meadows fringing the lake basin causes a significant reduction in resuspension, which combined with particulate trapping, results in increased water clarity over seagrass (Adams et al. 2016b). TSS concentrations in coastal lakes therefore primarily impact on the lower depth limits of seagrass meadows, especially in regions away from the ocean entrance.

## 14.4 Seagrass Community Metabolism and Morphology—*Zostera Muelleri* Case Study

The opportunistic seagrass *Zostera muelleri* is the primary species present in the south-east region, occupying a highly variable niche in terms of hydrodynamic and water quality stressor gradients. In the preceding sections we have presented an overview of the stressor gradient and seagrass distribution in the different systems of the region. In this section we explore the different strategies that allow *Z. muelleri* to successfully cope with such high variability in environmental conditions. Broadly, these can be divided into morphological responses to spatial environmental gradients and longer term temporal gradients (e.g. seasonal shifts), and physiological responses to shorter term gradients and stochastic disturbances (Maxwell et al. 2013).

### *14.4.1 Gross Primary Productivity (GPP)*

The areal rate of GPP integrates cellular scale photosynthetic responses, biomass density, and feedbacks associated with hydrodynamics, water quality and substrate quality. A close relationship between areal GPP and total biomass (above ground + below ground biomass: AGB + BGB) has been observed for *Z. muelleri* in a NSW coastal lake (Ferguson et al. 2017), indicating that rates are closely related to biomass density. Standing stocks (hence GPP) have been found to integrate light history over approximately 4 monthly timescales (Adams et al. 2015), with highest biomass and GPP rates occurring at the peak of 4 month integrated light in late summer. Interannual variation in factors influencing seasonal water quality (e.g. rainfall and wind) can have a profound impact on the expansion or contraction of *Z. muelleri* meadows, particularly in locations near the threshold of minimum light requirements.

Observations of areal biomass for *Z. muelleri* across nutrient gradients within the south-east region support the generalised model proposed by (Collier and Waycott 2014), whereby both shoot density and leaf length increase with nutrient supply. The oceanic dominated regions of eastern Moreton Bay support significant meadows of *Z. muelleri* with <25% cover and AGB of <15 g DW $m^{-2}$ (Roelfsema 2014), while the more fluvially influenced western bay supports denser meadows with ~25–50% cover and AGB of ~30 g DW $m^{-2}$ (Maxwell et al. 2013). Moving further south, the oligotrophic Lake Macquarie supports 76 g DW $m^{-2}$ compared to the mesotrophic Tuggerah Lakes with 130 g DW $m^{-2}$ (Ferguson et al. 2016). The nutrient status of Lake Macquarie is likely to be similar to that of Moreton Bay, therefore differences in standing stocks between these systems may reflect a latitudinal difference in performance in *Z. muelleri* due to temperature and light effects.

The ratio of AGB to BGB in *Z. muelleri* is also significantly moderated by the nutrient status of its environment. In nutrient-limited settings with low ambient nutrient concentrations in the water column, seagrasses tend to have much lower AGB:BGB due to the upregulation of BGB in order to access nutrients from porewaters (Perez et al. 1994). This effect was found to account for most of the variation in AGB:BGB in a study of *Z. muelleri* across depth gradients at multiple sites within the oligotrophic Lake Macquarie and mesotrophic Tuggerah Lakes (Ferguson et al. 2016).

### *14.4.2 Net Community Metabolism*

Net community metabolism (NCM; as measured by oxygen metabolism) refers to the net diel oxygen balance of a seagrass community. NCM here is defined by areal rates of GPP—PR—sediment oxygen demand over a diel cycle[1]. The sediment oxygen demand incorporates oxygen consumption due to the aerobic decomposition of OM detritus, as well as the oxidation of reduced sulphur and iron compounds resulting from the anaerobic decomposition of OM within the rhizosphere. Due to the potentially toxic effects of sulphide on seagrasses, balancing the oxygen demand exerted by sulphide oxidation is extremely important for determining survival of plants (Holmer et al. 2005; Holmer and Hasler-Sheetal 2014). In particular, sediment factors related to sulphide exposure (grain size and OM content) have been found to impact significantly on minimum light requirements of *Z. muelleri*, and may therefore be critical in determining the limits to distribution across sediment quality gradients (e.g. moving upstream in wave-dominated estuaries).

All seagrasses tend to reduce leaf area index across gradients of diminishing light (e.g. with depth or turbidity) in order to reduce self-shading (Collier et al. 2007). This is usually coupled with a reduction in BGB in order to reduce the metabolic burden of non-photosynthetic tissue (Hemminga 1998). The net result of these two responses is an increase in the AGB:BGB with reduced light, however the magnitude of the change in AGB:BGB is significantly moderated by the OM and fine sediment contents of the substrate due to negative feedbacks associated with sulphide exposure as outlined above (Ferguson et al. 2016).

The critical timescale for balancing NCM to ensure the survival of seagrass meadows is likely to be annual, given the seasonal swings in OM production and consumption in response to light, nutrient supply and temperature (Ferguson et al. 2017). It appears that various seagrass species can weather periods of negative NCM (and storage of reduced sulphur compounds within the rhizosphere) during winter, provided that these periods are balanced by positive NCM during summer months (Frankignoulle and Bouquegneau 1987). Potential stresses associated with allochthonous OM inputs to the sediment oxygen demand pose a significant risk to

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[1] Also referred to as the productivity: respiration ratio (P:R)

the maintenance of balanced NCM in estuarine settings where the relative influence of catchment inputs is greater compared to oceanic waters (e.g. fluvial delta shoals).

A compilation of metabolism measurements for *Z. muelleri* indicates that despite a wide range of GPP and PR rates, NCM is generally balanced (Duarte et al. 2010). Examples of negative NCM in *Z. muelleri* meadows are rare, and tend to be in environments that support ephemeral meadows (Eyre and Ferguson 2002). We suggest therefore, that while *Z. muelleri* benefits from a constant nutrient supply in estuarine environments, it can only persist in settings where it can maintain a balanced NCM over annual timescales. The importance of NCM to the maintenance of seagrass at the meadow scale is analogous to the significance of 'compensation point' at the plant scale, and it is likely that both measures are important in determining the distribution of *Z. muelleri* in the highly dynamic estuarine niche of the south-east region.

## 14.5 Summary

The observed distribution of various species of seagrass in the region are a result of interactions between seagrass processes and key environmental stressors (light, water quality, water flow) (Fig. 14.1).

The interactions between external stressors and internal processes are critical to survival. Negative feedback between seagrass in factors such as substrate stability, temperature, excess nutrients and light tend to limit distribution of particular species. Positive feedbacks such as trapping of particulate nutrients, suppression of sediment resuspension and groundwater inputs are important in shallow oligotrophic systems.

The presence of strong negative relationships between *Z. muelleri* and dissolved organic nitrogen and dissolved ammonia is strongly suggestive of some form of nitrogen toxicity in intermittent lagoons.

Estuary type, with the implicit relationships to catchment delivery (volume, quality and mode), entrance condition, recolonization potential and hydrodynamics has a strong controlling influence on the abundance and species composition of seagrasses. The largely (naturally) oligotrophic status of estuaries in estuarine-nearshore coastal continuum of the south-east region of Australia has implications for the nutrient regime and form of delivery that has shaped the seagrass assemblages in the region. The influence of estuary type also influences expectations about the occurrence of seagrass, it sets limits on the type and abundance of seagrass that can be expected to occur in different settings, with implications for future management targets.

Anthropogenic changes that affect the hydrodynamic and water quality (Fig. 14.7) regimes have the potential to affect both abundance and species of

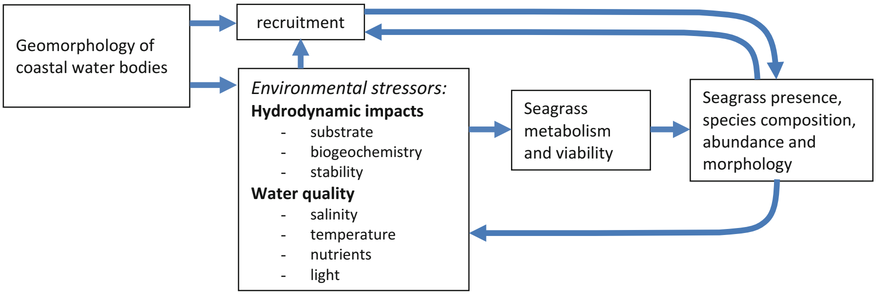

**Fig. 14.7** Linkages between geomorphology, environmental stressors and seagrass in the ENC zone. The stressors associated with hydrodynamics are those that are directly influenced by hydrodynamic energy

seagrasses present, often by subtle and sometimes non-linear processes. This also has important implications for management and rehabilitation of seagrass ecosystems.

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# Chapter 15
# Mapping, Monitoring and Modelling Seagrass Using Remote Sensing Techniques

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**Abstract** This chapter explains the types of information on the biophysical properties of seagrass and its surrounding environments, which are able to be measured, mapped, monitored and/or modelled using remote sensing techniques. This includes specifying the environmental conditions where these approaches do not work. “Remote sensing” refers to the use of a sensor not in direct contact with the target to measure one or more of its bio-geo-physical-chemical properties. This includes measurements from satellites, airborne, and remotely operated or autonomous above- and below-water systems. Six key topics are covered to show how

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remote sensing and its integration with ecological field survey methods, ecological theory and modelling, is an operational and accessible tool. Chapters 7, 9–11 in this book are complementary as they explain the biological and physiological bases of seagrasses and how they interact with light. The text is written from ecological perspective to explain “how to” implement remote sensing approaches at scales relevant to science and management problems. Specific details are presented for mapping and monitoring seagrass: extent, composition and biophysical properties from plant to rhizome and regional scales over $10^3$ $km^2$.

## 15.1 Introduction

Understanding how seagrass ecosystems change over time and space, provides the basis for developing and testing our knowledge of seagrass biology and ecology, and ultimately the development and assessment of seagrass management strategies. All forms of ecology and environmental management require data to be collected for seagrass properties over suitable areas and timescales—this chapter provides a basis for doing this using remote sensing. In this context remote sensing is any observation or measurement made at a distance from an object, and includes sensors in aircraft, drones, satellites and visual observations from aircraft and boats. The chapter aim is to explain and demonstrate the types of information, on the bio-physical properties of seagrass and its surrounding environments, which are able to be measured, mapped, monitored and/or modelled, using remote sensing techniques. It also identifies the properties which cannot be mapped and measured, and the circumstances under which these data and approaches cannot be used, and field survey or modelling are required. An on-line and interactive version of this material for seagrasses can be found at: www.rsrc.org.au/rstoolkit.

In this context remote sensing refers to the use of a sensor not in direct contact with the target to measure one or more bio-geo-physical-chemical properties. The majority of applications presented are from satellite and airborne platforms, with a smaller set from above- or below-water UAV’s, instrumented buoys, and will include sensors carried by people in the field and used in the laboratory. The review does not cover acoustic sensors, and the reader is referred to Foster et al. (2013) to cover suitable material from coral reefs and seagrass.

Compared to terrestrial applications, a small, but comprehensive body of literature has already been published on the structural and physiological properties of seagrasses and their environments that can be measured using remote sensing techniques. Readers are referred to Larkum et al. (2006), specifically chapters by Zimmerman (2006), Zimmerman and Dekker (2006), Dekker et al. (2006) and other key references such as Kirk (1994) for more detail. Later summaries show how remote sensing mapping has developed focussed on mapping seagrass properties, rather than scaling up and mapping physiological and structural properties (Ferwerda et al. 2007; Hossain et al. 2015). Key concepts from these papers are used in this chapter to explain how to collect appropriately scaled remotely sensed data and process it to map and monitor specific bio-geo-physical-chemical properties. This will be done by using the following objectives to explain and demonstrate:

(1) How seagrass properties [extent, composition, structure and function] are able to be "remotely sensed" from a variety of remote sensing instruments;
(2) How seagrass properties are measured and mapped;
(3) How seagrass properties are modelled;
(4) How the environmental properties controlling seagrass extent and condition are mapped and modelled;
(5) How seagrass properties are monitored over time; and
(6) Current research directions—addressing limitations and new technologies and techniques.

We focus on the six topics listed above as remote sensing and its integration with ecological field survey methods, ecological theory and modelling, has now matured to a widely operational and accessible tool. Remote sensing has become essential for mapping, monitoring and modelling in most environments. However, we lack detailed resources on "how to" implement these approaches at spatial and temporal scales relevant to the scientific and management challenges in seagrass environments. This chapter provides fundamentals of seagrass remote sensing and the means to link the science and applications. Mapping and monitoring seagrass properties from plant to regional scales using field and image measurements is possible using more than one approach—but needs to be done the right way.

Previously published work on remote sensing of seagrass treated remote sensing as an exploratory tool and often presented it in a form that was difficult to access and use by those concerned with seagrass ecology and management. We now have the data and tools in forms that can be learnt and applied by a wide group of people.

## 15.2 Remote Sensing of Seagrass Environments—Why We Can Use Remote Sensing to Map, Measure and Monitor Seagrasses

Interactions of light and other forms of electromagnetic radiation (EMR), with the environment are the fundamental basis for collecting and analysing all remotely sensed data. Algorithms are applied to each pixel in an airborne- or satellite-images to convert measurements of absorbed and scattered light into biological, chemical and physical features. In this context, light, mainly sun-light, acts as the key component of the remote sensing process, as it is either absorbed, scattered or transmitted by the gas, liquid or solid it is interacting with (Fig. 15.1). Seagrasses and the environments they occur within, produce a range of light interactions which are controlled by their biological and physical attributes. The biological and physical attributes of seagrass that control these interactions are associated with

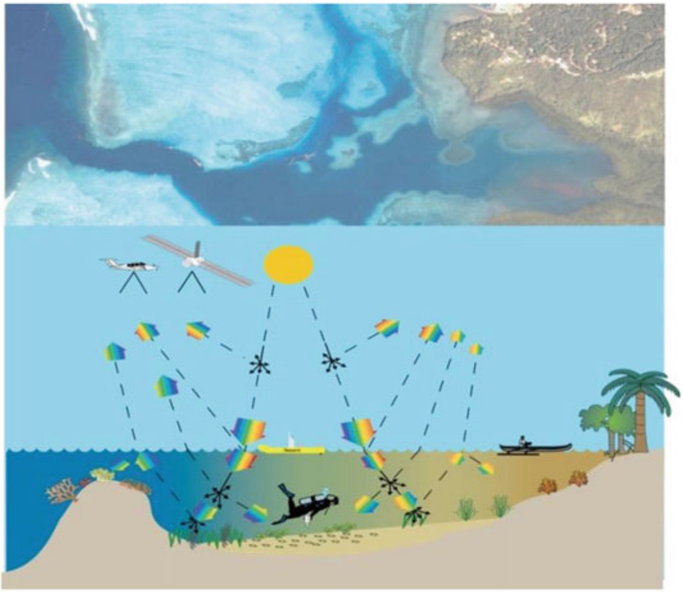


**Fig. 15.1** Light interactions in a coastal—estuarine coral-reef and seagrass environment in coastal Viti Levu, Fiji, with a the top panel showing a true colour Quickbird-2 image with 2.4 m pixels and lower panel showing a cross-section of the imaged area, including the source(s) and interactions of light that control measurements of seagrasses made from remotely sensed data

their structure, chemistry and physiology, and are very well understood (see Chaps. 11–13 in this book) down to molecular levels. Our chapter builds on that understanding to explain and demonstrate how seagrass properties are able to be "remotely sensed" from airborne and satellite images to map and monitor seagrass properties at specific spatial and temporal scales. Our focus is mainly on optical or passive remote sensing systems which rely on sunlight as the source of EMR illuminating seagrasses and their environment.

The subject of light interactions with seagrass and its surrounding aquatic environment has been dealt with extensively at the scale of individual plants (Kirk 1994; Zimmerman 2006) and cellular and photosystem levels (Larkum et al. 2006). However, very few studies link this knowledge to mapping and monitoring. Previous seagrass remote sensing was driven by the availability of specific types of airborne and satellite image data, at specific spatial and temporal scales. This chapter links the understanding of light interactions from within plant or shoot ($10^{-3}$ $m^2$) to regional and national ($10^6$ $km^2$) scales—for using remote sensing to map and monitor seagrass environments over these scales. However the mapping and monitoring approaches used do have physical limits, because this approach relies on measuring reflected light, so this creates a limitation on the places it can be used due to:

1. depth of water
2. clarity of water
3. small and cryptic species.

This means that for a very large component of tropical Australia (particularly shallow sub-tidal coastal areas) remote sensing techniques may be of limited applicability where turbid water and small species lead to limited ability to reliably detect and map seagrasses. There are a range of alternative field based approaches to mapping and assessment in these cases that have been employed to successfully generate seagrass maps over a range of spatial scales.

- Camera based tows in deep-water (Carter et al. 2016);
- Rapid assessments of intertidal locations of small cryptic species—helicopter/free diving etc.

Seagrasses interact with sun-light in similar ways to terrestrial plants, however they have different leaf morphologies and canopy structures, as well as relative levels of photosynthetic and accessory pigments. In addition, for the majority of their life, they sit completely submerged in the water column, and are partially or fully exposed under some tidal conditions. There are also significant differences between and within seagrass species in terms of growth forms and function, that yield different physical structures and chemical compositions. These differences result in unique scattering and absorption signals, and hence their detection in airborne or satellite images is possible within a certain range of water depths, water column clarities and seagrass cover levels. As noted before, and in published literature (Green et al. 1996; Phinn et al. 2008), if seagrass are in locations with clear water >15 m deep, or where water clarity is reduced by suspended or dissolved materials, or at low cover levels (<20%) it is not likely to be able to be mapped from airborne or satellite remote sensing. By measuring these sun-light interactions, we can infer or measure properties of seagrass. This approach is scale specific and each of the scales and their controlling bio-chemical and structural properties is outlined in Table 15.1. It is also pertinent that aquatic radiative transfer is considered at this point as seagrasses sit in an aquatic medium that changes its content and scattering/absorption properties rapidly.

Previous works have defined in detail, down to canopy, stem architecture, leaf structure and photosystem level, how light interacts with seagrasses (Zimmerman 2006). This chapter explains how algorithms and approaches for mapping critical seagrass properties and monitoring changes over time work, so they can be used for science and management in an appropriate way.

There is no comprehensive overview of how seagrass properties can be mapped and monitored using remote sensing, with reviews only providing application examples (Dahdouh-Guebas 2002; Ferwerda et al. 2007; Green et al. 1996; Hossain et al. 2015) or details on the biophysical properties of light interaction (Larkum et al. 2006). To address this we take a holistic approach to explain how to map

**Table 15.1** Scales of seagrass biological and physical properties and their measurement using remotely sensed data

| Seagrass organization level [spatial scale (min-max)] | Temporal scale | Individual (internal) process controls | External process controls | Field measurement—structure | Bio-chemical controls on EMR interactions | Structural controls on EMR interactions | Published examples |
|---|---|---|---|---|---|---|---|
| Shoot/clone (~1 mm–~50 cm) | Daily, monthly, annual | *No spatial variability* within shoot properties<br>*Process controls*: Photosynthesis/growth-respiration, nutrient uptake | *Temporally varying* ambient or "around shoot" process controls<br>*Process controls*: light, temperature | Leaf, root | pigment types, Pigment concentrations | Internal leaf structure, leaf morphology, growth form | Elkalay et al. (2003) |
| Shoots to patch (>50 cm–1 m) | Daily, monthly, annual | (1) *Spatial variability between shoot properties (species, size, age)*<br>(2) *Spatial variability between shoot properties of the patch*<br>*Process controls*: Growth/shoot production, photosynthesis, growth rate, elongation rate, respiration, mortality, leaf loss rate, belowground loss rate, regression, lateral dispersal, reproduction, flowering-seed production, seed germination, seed (survival, viability, dormancy, emigration, immigration), nitrogen uptake, carbon transfer, shoot ageing, reclaimed nitrogen rhizome branching rate, rhizome branching angle | (1) *Temporally varying "around shoots"* process controls (2) *Spatially and temporally varying "around patch"* process controls<br>*Process controls*: Hydrodynamics, wave height, current velocity, wind speed, wind generated currents and waves, light, saturation light intensity, turbidity, sediment movement, sediment composition, scouring (disruption of sediment dynamics), temperature, salinity, depth, shoaling effect, emersion period, sulfide toxicity, desiccation stress | Rhizome, root, seed, leaf, shoot, ramet, patch | Pigment concentrations, optical properties of water | Growth form, canopy form | Bearlin et al. (1999), Creed (1999), Fonseca et al. (2002), Kendrick et al. (2005), Koch et al. (2007), Larkum et al. (2006), Plus et al. (2003), van der Heide et al. (2010), Verhagen and Nienhuis (1983) |

(continued)

**Table 15.1** (continued)

| Seagrass organization level [spatial scale (min-max)] | Temporal scale | Individual (internal) process controls | External process controls | Field measurement —structure | Bio-chemical controls on EMR interactions | Structural controls on EMR interactions | Published examples |
|---|---|---|---|---|---|---|---|
| Patch/ Patches | Daily, monthly, annual | *Spatial variability between patch properties*: patch growth rate, patch size, patch age, peripheral growth, edge dynamics, shoot composition<br>*Process controls:* Growth, mortality | *Spatially and temporally varying "around patches"* process controls<br>*Process controls*: salinity, freshwater inflow, water level, current velocity, light, light reaching seagrass beds, temperature, sediment nutrients, sediment phosphate, water column nutrients, water column phosphate | Biomass per unit area | Pigment concentrations, optical properties of water | Growth forms, canopy forms | Fong and Harwell (1994), Larkum et al. (2006), Wortmann et al. (1997) |
| Meadow | Seasonal (3–4 months) to annual | *Spatial variability within meadow properties: shoot properties* (size, age, density, biomass, species), *if made up of patches then spatial variability between patch types* (type determined by shoot properties)<br>*Process controls*: clonal growth (rhizome elongation, branching rate), radial extension via rhizome growth, shoot mortality, growth, mortality | *Spatially and temporally varying "around meadow"* process controls<br>*Process controls*: relative exposure index, Physical disturbance, hydrodynamics, wave exposure | Shoots, rhizome, patch, presence/ absence | Pigment concentrations, optical properties of water | Growth forms, canopy forms | Kelly et al. (2001), Kendrick et al. (1999), Larkum et al. (2006), Sintes et al. (2005, 2006) |

(continued)

**Table 15.1** (continued)

| Seagrass organization level [spatial scale (min-max)] | Temporal scale | Individual (internal) process controls | External process controls | Field measurement—structure | Bio-chemical controls on EMR interactions | Structural controls on EMR interactions | Published examples |
|---|---|---|---|---|---|---|---|
| Regional meadows | Seasonal (3–4 months) to annual, decadal | *Spatial variability of properties between meadows: according to meadow types* (determined by meadow properties as shown in internal process controls for meadow)<br>*Process controls*: species, percentage cover, abundance, density | *Spatially and Temporally varying process controls between* (1) *meadows/ sections or* (2) *meadows of varying seagrass habitat types based on location setting*<br>*Process controls*: REI (relative exposure index), MSL (mean sea level), sediment composition, wind, depth, temperature, | Meadows, presence/ absence | Pigment concentrations, optical properties of water | Growth forms, canopy forms | Carruthers et al. (2002, 2007), Fonseca et al. (2002), Kilminster et al. (2015), Larkum et al. (2006), Lyons et al. (2012, 2015), Phinn et al. (2008), Roelfsema et al. (2014), Saunders et al. (2015) |
| Coastal ecosystem | not determined (decadal, century?) | *Spatial variability between types of regional meadows*: regional meadow types (determined by regional meadow properties as shown in internal controls for regional meadows) | *Spatially and temporally varying process controls between regional meadow types.*<br>Process controls: Season, Geographical section, Light availability, Substrate suitability, Temperature, Tides, Flood plume, Wave | Meadows, presence/ absence | Pigment concentrations, optical properties of water | Growth forms, canopy forms | Carruthers et al. (2002, 2007), Grech and Coles (2010, Kilminster et al. (2015), Roelfsema et al. (2009, 2014) |

Seagrass organization level [spatial scale (min-max)] = maximum and minimum area covered by seagrass form
Temporal scale—time scale on which the seagrass form listed in column 1 undergoes changes
Individual (internal) process controls—biological and physical processes affecting the seagrass form listed in column 1
External process controls—processes eternal to the seagrass form controlling its growth and mortality
Field measurement—structure—features of the seagrass form listed in column 1 able to be measured in the field
Bio-chemical controls on EMR interactions biological and chemical properties of the seagrass form listed in column 1
Structural controls on EMR interactions—physical structural controls on the seagrass form listed in column 1

seagrass based on the interactions outlined above. Since the most recent assessment of the physical and biological basis for remote sensing for seagrass in Larkum et al. (2006), there has been significant progress in: (1) access to a range of publicly available satellite image and field data sets; (2) increasing the spatial and radiometric details of images; (3) accuracy and availability of algorithms for mapping the composition of seagrass environments and biophysical properties on very high spatial resolution and/or very long time series; (4) availability of algorithms for biophysical property estimation linked to the field data; (5) access to open-data, -software and on-line processing for image processing; and, (6) operational use of map products for management activities.

Taking this assessment as a building block and using the conceptual framework outlined in Table 15.1 to relate remotely sensed measurements to seagrass properties at specific scales, we aim to equip our readers with enough information to:

- understand considerations for deciding whether to use or not use remote sensing;
- interpret remotely sensed products for seagrass environments;
- use remotely sensed products to map and/or monitor seagrass properties; and
- assess maps of seagrass properties produced from airborne or satellite images to determine if they are correct, if they are accurate, and where they do and do not work.

## 15.3 Fundamentals: Sensors, Mapping and Validation

To understand how information is extracted from remote sensing data, we explain how the data are collected from a range of sensor types, then how these data are analyzed and verified to produce maps that allow the measurement and monitoring of seagrass properties. Three sections are used to explain this:

- Sensor and Platforms Types and Dimensions
- Information Extraction Approaches: Mapping and Modelling
- Essential Fieldwork and Data

### *15.3.1 Sensors, Platforms Types and Dimensions*

Remote sensing instruments and platforms used to map and monitor seagrass properties vary in multiple dimensions. A common division of these sensors is into passive and active technologies. For seagrass, passive sensors measure visible or thermal EMR reflected or emitted from a surface, such as seagrass leaves. Active instruments, such as radar (radio detection and ranging), lidar (light detection and

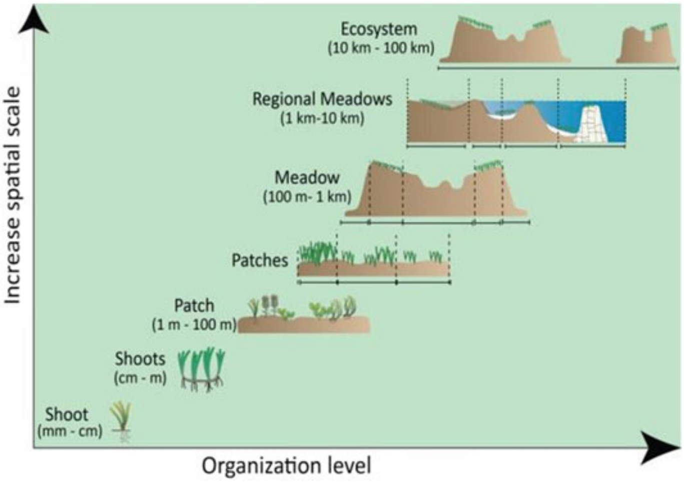


**Fig. 15.2** Specific scales of seagrass structures and processes in spatial and temporal contexts

ranging) and acoustic sensors, emit EMR that after reflection is returned to the sensor. Active systems measure both distance to a target/pixel and its reflectance.

Biophysical properties of seagrass are required at various levels of detail from individual shoot up to whole ecosystem level (Fig. 15.2; Table 15.1). At each hierarchical level seagrass properties interact differently with EMR due to their dominant structures, processes and chemical compositions evident at that spatial scale.. Selection of an appropriate image data set and processing algorithm should be matched to the spatial, spectral and temporal scale(s) of the feature(s) you are aiming to map (Fig. 15.2). These considerations include characteristics at spatial (leaf/patch/meadow), spectral or type of light (presence/absence/species), and, temporal (seasonal/annual) scales.

The spatial characteristics of seagrasses which may be mapped are controlled by pixel size and scene extent, (Figs. 15.2c, 15.3; Table 15.1). Pixel size is commonly characterised as very high (<0.5 m), high (0.5–10 m), moderate (10–50 m) and low (50 m–km) spatial resolution. Depending on the acquisition platform, image scene extents can vary in size from several km$^2$ to tens of thousands of km$^2$.

Spectral characteristics of remote sensing data, relates to the location, number and width of bands along the electromagnetic spectrum. Here, multi-spectral imagery is comprised of <10 broad (>10 nm) bands, whilst hyper-spectral is characterized by >10 narrow (<10 nm) bands. Band placement and band width, especially the in visible range of the electromagnetic spectrum, are important considerations when attempting to differentiate submerged features such as seagrass. This requires careful choice of band location and width to maximize discrimination, but minimize the effects of the water column.

Temporal characteristics of a satellite's orbit, i.e., time between over-passes, define the minimum revisit time of the remote sensing instrument to any given point

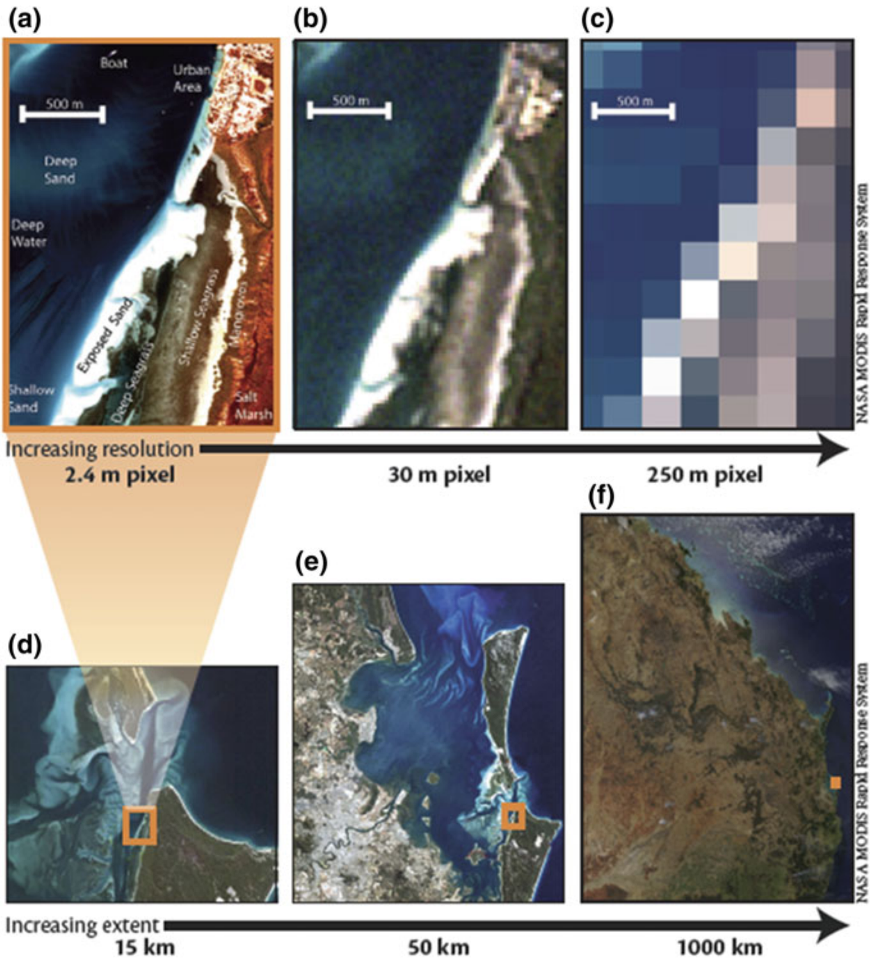


**Fig. 15.3** Imaging sensors with increasing pixel sizes over coastal seagrass environments

on the earth's surface and the time of day or night of image capture (Fig. 15.3). This can vary from hours for airborne sensors, to days, weeks, and years for satellites. Next to sensor type, temporal considerations when planning a seagrass remote sensing data acquisition need to include: tidal stage, solar and sensor geometry, sea state, water clarity, and phenology of the seagrass and other marine plants.

The choice of platform to map the biophysical properties of seagrass s is driven by the required spatial, temporal and spectral characteristics of properties to be measured. Most common platforms are satellite or airborne, with the latter including airplanes, helicopters, and Unmanned Automated Vehicles (UAV). On the ground or in-water, passive and active systems have also been used along with acoustic systems. Automated Underwater Vehicle (AUV) are increasingly being used in marine environments as well to acquire imagery of the seagrass habitat. UAV and airborne systems can be flown when required and conditions are suitable. For satellite sensors, publicly available moderate- to low- spatial resolution sensors capture data continuously on regular cycles from 1–16 days, while high spatial resolution satellites will only capture areas on request, but can repeat within 1–5 days.

The image data sets outlined above can be obtained from a range of public-access and commercial outlets for local sites to global scales. Satellite image data archives, with pixel sizes >20 m, including the Landsat series, SPOT and MODIS, are available at both global and national scales, in the form of un-processed images and biophysical map products. A regularly updated overview of these data and products, and links to download sites are presented in the Committee on Earth Observation Satellites Handbook (CEOS 2015) (www.eohandbook.com/). The major space agencies (NASA, ESA, JAXA) all maintain EO data viewers and portals to enable search, selection and download of these archives over set areas, with private companies also providing access to these data streams, e.g., Amazon. The most recent trend in remote sensing data processing is to access peta-byte scale on-line stores of these global image archives, and to process them on-line then download map products off-line. Examples include Google’s Earth Engine at a global scale, and the data cube concept at the national scale, such as Australia’s Geoscience Data Cube. Governments also maintain national aerial photo and image archives which can be accessed on-line. Private agencies, such as DigitalGlobe, maintain high spatial resolution (<5 m) satellite image archives, extending to the early 1990s, and collect new data on request for set fees and for use under licence (Fig. 15.4).

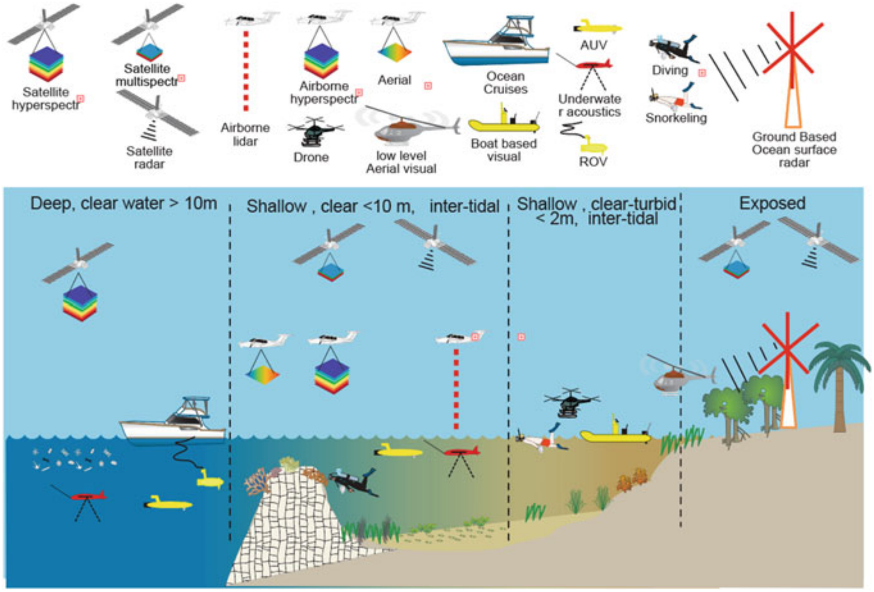


**Fig. 15.4** Platforms used to collect remotely sensed data to map and monitor seagrass and their surrounding habitats

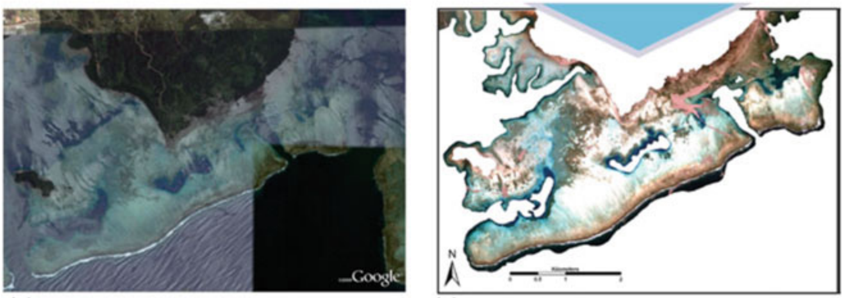
### *15.3.2 Information Extraction Approaches: Mapping and Modelling*

Once appropriate airborne, satellite or other image data have been obtained, moving towards extracting a map or a series of maps of seagrass properties requires three stages of data processing. The first two, image pre-processing or corrections, and information extraction, are outlined below. Information extraction can take one of two forms, producing maps of: (i) thematic (categorical) output (e.g., seagrass species), or (ii) quantitative output (e.g., seagrass height, biomass, percentage cover). The map validation or verification stage, to quantify the accuracy of the map products is then outlined in this Section.

Before any thematic or quantitative information is extracted from remote sensing imagery, pre-processing is required so that the image data is correctly positioned on the ground to allow integration with other data and that the pixel values accurately represent the amount of light being reflected or emitted from the water surface or seagrass (Dekker et al. 2005). Geometric corrections to produce georeferenced images are required when analysing a sequence of images of the same area over time and for linking field measurements (e.g., plots, transects or other measurements) to image data for mapping, validation and modelling. Commercial and open-source image processing or GIS software provide geometric correction utilities. Images can be purchased with or without these corrections, and the level of corrections applied is listed in the image meta-data files (Fig. 15.5).

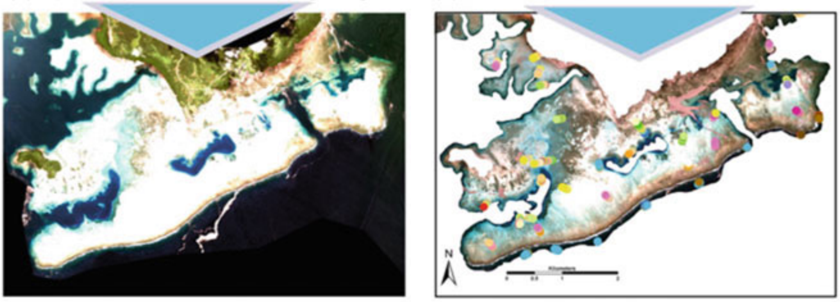
Radiometric corrections are used to eliminate variations in pixel reflectance values or signatures produced by atmospheric conditions, different sun and sensor angles, and water surface and depth. This is required for the delivery of pixel reflectance values or signatures that accurately represent surface or sub-surface spectral-signatures at the time of image acquisition. This type of correction is essential if radiative transfer equations are used to transform the pixel value to a biophysical quantity, e.g., water depth or leaf area index, to distinguish features (e.g., seagrass species); and to examine changes over time. For a full description of these corrections readers are referred to Green et al. (1996), Hedley et al. (2005).

This includes three types of corrections—sun-glint, air-water interface and water depth. Sun-glint is direct specular reflectance from the water surface due to specific sun illumination and sensor viewing angles in relation to the water. These effects can be limited to waves at certain viewing angles, or in the worst case produce large hot-spot flares covering most of an image. This can be avoided by timing image acquisitions to reduce hotspots, or reduced after image acquisition (Hedley et al. 2005). The air-water interface affects light as it travels through the atmosphere-water boundary and this can be corrected using a physics-based (Brando and Dekker 2003) or an empirical (Andréfouët et al. 2003) algorithm. Water column or depth correction, requires estimating and then compensating for light absorption and scattering that occurs as sun-light illuminates and is then reflected from the sea-floor; it can be conducted using inverse radiative transfer



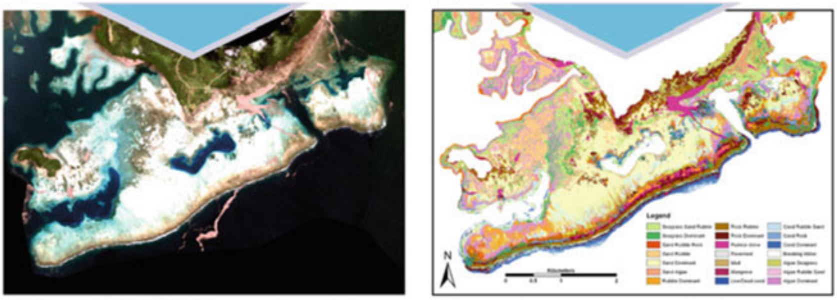
**(a)** Exploratory - on-line databases, e.g. Google

**(e)** Land and deep-water area masked out



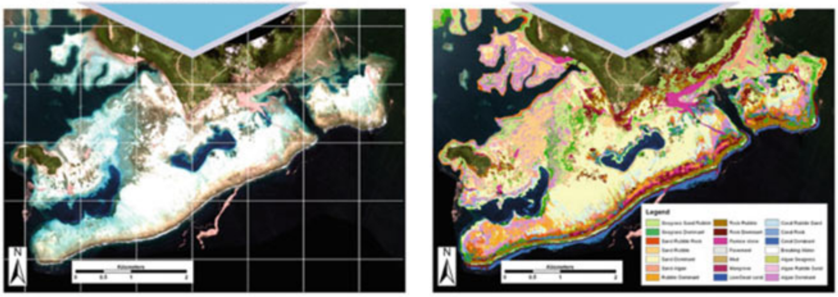
**(b)** Raw Quickbird image - no corrections

**(f)** Image with benthic cover field data



**(c)** Corrected Quickbird image - atmospheric and air-water interface correction

**(g)** Result from benthic cover classification



**(d)** Georeferenced image - fully corrected

**(h)** Final classification overlaid on image

**Fig. 15.5** Example of pre-processing and mapping project methods (Brando and Dekker 2003) or by creating empirical depth invariant bands (Lyzenga 1978, 1981).

***Thematic Data Products*** contain discrete categories (e.g., presence/absence, species type, and ranked or ordinal classes. e.g., seagrass cover 10–40%). Commonly used approaches are "pixel-based" or "object-based." Pixel-based supervised or unsupervised classifications use multivariate clustering algorithms to group pixels with similar spectral signatures and provide them with a thematic or categorical label. Object based image analyses first segment the image into "objects" based on similar spectral and textural characteristics. Next each segment or object is assigned a label based on its spectral, textural, locational and biophysical properties (Blaschke et al. 2011). As with geometric and radiometric corrections commercial and open-source image processing or GIS software provide functionality to implement these classifications.

***Quantitative Data Products*** have continuous interval or ratio level values (e.g., biomass, percentage cover, depth) and are derived from empirical, physical, or biological models. Empirical models develop a relationship between the spectral reflectance characteristics of a pixel and the relevant field measurement(s). Physical models derive continuous information based on inversion of the radiative transfer theory replicating the light path from the sun, via the atmosphere and water column and back to the remote sensing sensor. Physics-based approaches require the optical characteristics of the atmosphere and water column surrounding the seagrass environment, and spectral reflectance signatures characterising the features making up the seagrass environment (e.g., seagrass species, sediment types). This type of model has an advantage over empirical models in that it provides information on seagrass composition and abundance, as well as physical information (e.g., water depth and quality). Physics based models can be used to assess the ability to differentiate seagrass species under varying sensors or environmental conditions (Hedley et al. 2005; Mobley 1994).

Once you have a thematic (e.g., seagrass species composition) or quantitative (e.g., seagrass biomass) map and which may be produced repeatedly for the same area at different times, change in the spatial patterns and values of seagrass properties can be assessed. This is done by multi-temporal analysis approaches, which can examine the difference between maps on two or more successive dates. These approaches are becoming ever more feasible as satellite remote sensing image archives, such as that from the Landsat program (1972—present), are made accessible (Wulder et al. 2012). Temporal analysis of seagrass, requires careful consideration of other environmental variables when conducting analyses, e.g., the water column can vary in composition in time and space, as well as in depth due to tidal fluctuations. While it is not always possible, temporally-separated marine image sequences should consist of data acquired under similar conditions (e.g., tidal height, water clarity) (Roelfsema et al. 2013).

### 15.3.3 Essential Fieldwork and Field Data

Remote sensing for mapping, monitoring and modelling seagrass or other benthic environments requires information from the field for establishing the mapping process (calibration) and for checking the accuracy of its results (validation). Field data collection not only provides quantitative information for calibration and validation, it provides also qualitative information that increases the producer's and user's understanding of the composition and dynamics of the seagrass environment. "Smelling the seagrass" provides a crucial part of any seagrass mapping, monitoring or modelling program. Often this is also referred to as "ground truthing", however we suggest this latter term not used as it is often taken to mean, that the measurements conducted in the field are 100% accurate (the "truth"), which is not the case. All of these measurements involve sampling at one level or another, hence "ground validation" is more preferable.

Ideally calibration and validation data sets are independent, to assure the validation process is considered un-biased from the calibration process. Calibration (training) data are integrated with the mapping and monitoring approach to create a map from the remote sensing imagery. Validation data are used to assess the errors and the accuracy of the output thematic or quantitative map products. Currently there is no remote sensing approach for mapping and monitoring seagrass habitat that does not require some type of field data (e.g., spectral bottom reflectance signatures, biomass). Similarly, validation always requires field data at some stage.

***Requirements for integrating field and image data***—Compatibility between the geo-locational data (projection, datum, coordinate system), thematic class types and mapped biophysical properties is critical if image and field based data are to be compared. Requirements firstly include reduction of spatial mis-registration errors, or spatial alignment, between field and image data; e.g., taking care that field data sets, spatial layers or remote sensing imagery are properly georeferenced to each other. The geo-locational data properties include a known coordinate system (e.g., Latitude and Longitude, or Easting and Northing) and geodetic datum or origin point (e.g., World Geodetic Datum 1984). Secondly, the field data require measurement units or thematic classes that are comparable with the final remote sensing products. For example seagrass cover in the field with a descriptive ranking (e.g., low, moderate, high) can only be compared to similar map data.

***Field program design and requirements***—Ideally the sampling design for field data collection will be statistically sound in terms of location(s) and number of sites, however it must also be logistically feasible, keeping in mind the available resources (Congalton and Green 1999). Sampling design includes specifying: sampling unit, sample distribution method and number of samples. The sample unit can be a point (e.g., along transect or spot checks) or area (e.g., pixel or group of pixels). The sample size is determined by the required accuracy of the final product. The sampling distribution within the study area is preferably random, although practically this is often challenging, and stratified and stratified random sampling can be used. From a remote sensing perspective sample locations and number of samples are directed from statistical sampling requirements to meet a certain error levels and locations chosen typically in a stratified process based on a visual assessment of groups of pixels that make up the remote sensing image.

***Field data collection methods***—A variety of field methods have been used to gather information characterising seagrass habitats for both empirical and analytic/deterministic approaches. Most empirical remote sensing based mapping approaches require information on seagrass species composition, abundance or biomass. This type of information has been gathered through different approaches ranging from spot checks, visual quadrat analysis, direct measurements of leaves, plants or plots or photo transects. These sampling units are applied to measure a number of properties: species type, %-cover, seagrass biomass cores, or leaf chemical content

Analytic remote sensing approaches require field data on the spectral absorbance, transmittance and reflectance characteristics of the water column and the features making up the seagrass habitat. This includes: water depth, attenuation and backscattering, total suspended solids, pigment concentration, and spectral reflectance of seagrass and algae species and bottom types.

***Validation of the image-based maps***—To assess the reliability of an image based seagrass property map, several methods can be used. They include: visual assessment of the patterns present, and calculating error and accuracy measures using validation data sets. Accuracy measures can be grouped into those used for measuring the agreement between reference data and mapped data for continuous maps (e.g., biomass) and thematic maps (e.g., seagrass communities). Thematic maps are validated by creating an error matrix which describes the relationship between the map data and coinciding reference data (Congalton and Green 1999). The error matrix is used to calculate map error or accuracy measures (e.g., overall accuracy) and the individual thematic map category accuracy (e.g., user and producer accuracy) (Congalton and Green 1999). Continuous maps are validated using field data to calculate $r^2$ or root mean square error between estimated and measured data values. To assess these accuracy measures in comparison to other map products it is important that detailed information on the validation process is provided for both products (Congalton and Green 1999).

## 15.4 Mapping Seagrass

To choose an appropriate data set and mapping approach it is important that the producer and the user of the seagrass map (data) set understand what property of seagrass needs to be mapped. The next step is to work together to establish a suitable data set and mapping method to apply and deliver the required map. A mapping needs table is a one way of linking the requirements to be included in a map, with the most appropriate data and mapping methods (Table 15.2). The table requires input on: intended purpose of the map; which seagrass property is to be mapped; the extent of the area to be mapped; the smallest feature to be included in the map (i.e., minimum mapping unit size); required thematic mapping accuracy or acceptable parameter error level; required time period(s) to be mapped; and characteristics of the area to be mapped. Maps of seagrass properties are typically collected to address one of three fundamental ecological and management related questions. We present these three questions below; and then explain how these are derived in the following sections:

- Where is seagrass present?
- Which seagrass species are there?
- How much seagrass is there and what condition is it in?
- How is seagrass condition changing over time?

### *15.4.1 Where Is Seagrass Present?*

Understanding and management of seagrass as a part of coastal environments requires base knowledge of where it does and does not occur—as is common in most biogeographic studies. This requires mapping at meadow scales (Fig. 15.2) which can involve building on point or plot level measurements, and in some cases modelling, which is discussed in more detail as part of Sect. 15.5. Modelling is used more commonly to determine where seagrasses are most likely to occur and to fill in gaps where there are no field survey or suitable remotely sensed data due to water-depth or -clarity limitations.

***Scale of mapping***—Presence/absence maps are binary in form and show areas of seagrass or non-seagrass from local (km$^2$) to national ($10^4$–$10^6$ km$^2$) scales. These are not detailed benthic cover or habitat maps, however they can be derived from these more complex maps.

***Basis for mapping (assumption of algorithms used)***—From a purely airborne or satellite image approach, mapping presence/absence relies on the assumption that there is a significant difference between the spectral reflectance signatures of seagrass and non-seagrass areas. For large parts of northern Australia this may not be the case and alternative field based methods for mapping may be required where deep or turbid water and small and cryptic species mean that the utility of satellite based remote sensing is limited. In visual terms, this means that seagrass and non-seagrass areas are visible and have distinctly different colours, tones and textures. In terms of level of detail, it also assumes that seagrass occurs in homogenous patches that are significantly larger than the image pixel size and that the imaged area covers the area to be mapped.

***Approach and algorithms***—A progression of data sets and approaches are used for this mapping from simple to complex, using field data and aerial photography to multi- and hyper-spectral image data sets, with analysis from visual delineation, to interpolation of field data points, to image classification, and to image classification guided by field data.

At the least complex level, field data from point (e.g., drop camera images) samples with presence/absence observations collected with positional information

**Table 15.2** Mapping needs table, to be completed by producers and users of seagrass maps

| Required information to use remotely sensed data for monitoring | Your mapping or monitoring requirements? | | | | | | Other |
|---|---|---|---|---|---|---|---|
| Marine environmental variables (geomorphic, benthic, seagrass) | | | | | | | |
| Extent of area to be mapped and monitored | 0–50 $km^2$ | 50–250 $km^2$ | 250–500 $km^2$ | 500–5000 $km^2$ | 5000–50,000 $km^2$ | 50,000—$km^2$ | |
| Minimum size of feature to be mapped (i.e., the object you want to see) | Extremely fine <5 m | Fine 5–20 m | Medium 20–250 m | Coarse 250–1000 m | Extremely coarse >1000 m | | |
| Level of **minimum** measurement precision (i.e., smallest measurable change in % coral cover) | 0–5% | 5–10% | 10–25% | 25–50% | Anything | | |
| Level of **minimum** measurement accuracy (i.e., required acceptable agreement between estimated and actual value of % coral cover) | Anything | Low 10–40% | Medium 40–70% | High 70–90% | Very high 90–100% | | |
| Time period over which maps are to be updated (e.g., annually) | 1–24 h | 1 day | 1 week | 1 month | 3 month | 3–5 years | |
| Reason for mapping driven by | Once-off project (e.g., design harbour) | Once-off project, but recurring for other sites | Event based (e.g., bleaching, vessel grounding) | Continuos over time (e.g., 3 yearly seagrass cover) | Retrospective (e.g., mangrove dieback) | | |
| Access to study site | Easy | Only on demand | Difficult—too remote | Difficult—too many different sites | Dangerous (e.g., crocodiles) | No access | |

Complete each row independently

can be plotted on existing maps or interpolated to produce a map showing the extent of each benthic cover type. If suitable aerial or satellite image data are available, and areas of seagrass and non-seagrass are known, standard visual image interpretation cues or keys can be applied to manually delineate the boundaries of seagrass using GIS or image processing software (Purkis and Roelfsema 2015).

Image classification techniques, also applied through GIS or image processing software, can be used to automate this process. The map producer first identifies training pixels on the image where seagrass occur, often guided by field data, and then the image classification algorithm identifies all other pixels in the image with similar spectral reflectance signatures to the target seagrass pixels. This approach can be improved by use of field data locations to help train the classifier, and the use of patterns or contextual information to refine the accuracy of the classification (Purkis and Roelfsema 2015).

### *15.4.2 Which Seagrasses Are There?*

Mapping seagrass species or community composition is the next level of detail from seagrass presence/absence and uses the same base data sets and mapping approaches. In this context the output maps are no longer binary, but now contain thematic or categorical information about benthic cover type, e.g., seagrass species or commonly occurring species assemblages. This does require more complex image and field data be used in combination, along with more advanced image processing algorithms (Hossain et al. 2015; Phinn et al. 2008; Roelfsema et al. 2014). Modelling is also used to fill gaps where there are no field survey or suitable remotely sensed data due to water depth or clarity limitations. Many Australian seagrass species may appear to be quite similar from remote sensed data due to similar growth forms and separation may not be possible to species level for some using these techniques (e.g., *Halodule uninervis, Zostera muelleri, Cymodocea rotundata*). In these circumstances it may be more appropriate to rely on field based assessments if species change is an important question.

***Scale of mapping***—Maps showing individual seagrass species and commonly occurring seagrass species assemblages are typically produced over scales of site ($10^2$ $m^2$) to sub-regional ($10^3$–$10^4$ $km^2$) levels.

***Basis for mapping (assumption of algorithms used)***—Mapping seagrass species and community composition from airborne or satellite images assumes there are significant differences in spectral reflectance signatures or spatial patterns between the types of seagrass species and that seagrass species and/or assemblages occur in homogenous patches that are significantly larger than the image pixel size. As with presence/absence mapping, this means that patches of different seagrass species are assumed to have distinctly different colours, tones and textures, which is also indicated by their different signatures. Where this is not the case a higher reliance on field based methods for mapping may be required.

***Approach and algorithms***—Similar data sets and algorithms are used in this section as with presence/absence mapping, however in this context they need to be more refined. Starting at the least complex level, field data from point (e.g., drop camera) samples with dominant type of benthic cover or percentage cover observations per species, collected with positional information, can be collected and plotted on existing maps or interpolated to produce a map showing the extent of each benthic cover type. The seagrass species type or community composition classes can also be mapped by standard visual image interpretation cues or these keys also can be applied to manually delineate the boundaries of seagrass species using GIS or image processing software.

Image classification techniques, can be applied by the map producer first identifying training pixels on the image where certain seagrass species are known to occur, guided by field data, then the image classification algorithm identifies all other pixels in the image with similar spectral reflectance signatures to the target seagrass species pixels. This approach can be improved by use of field data locations to help train the classifier, and the use of patterns or contextual information to refine the accuracy of the classification (Purkis and Roelfsema 2015). Most recently species and community composition mapping has moved to object based image analysis, which enables delineation and identification of groups of pixels as seagrass species (Roelfsema et al. 2014). This approach uses similar cues to manual approaches, especially texture and context, that combine the characteristics of individual pixels or groups of pixels.

### 15.4.3 How Much Seagrass Is There and What Condition Is It in?

Once the extent of the seagrass environment and its composition is known, there is a need to move to quantitative data on the structure and function of seagrasses to inform science and management. These data are significantly different to the presence/absence and composition maps in that the pixel values contain estimated quantities and are numeric in form. These properties include structural dimensions, e.g., height, percentage cover, leaf area index, biomass, and functional attributes e.g., absorbed photosynthetically active radiation.

***Scale of mapping***—Algorithms for estimating these properties produce polygons or pixels containing interval or ratio level quantities representing an estimated value of a seagrass biophysical property, e.g., above-ground biomass. These are not ranked categorical or thematic values, they are real numbers, and are produced from site ($m^2$) to sub-regional ($10^3$–$10^4$ $km^2$) scales.

***Basis for mapping (assumption of algorithm)***—Spectral reflectance signatures of seagrass species are a record of the scattering and absorption of light by the seagrass, which are directly controlled by the seagrass' physical structure, chemical composition and physiological state (Zimmerman 2006). Measured absorption or scattering can be inverted mathematically and used to estimate the seagrass biophysical property controlling it—for full details on this process see Zimmerman (2006), Kirk (1994). This approach requires seagrass species and/or assemblages to occur in homogenous patches that are significantly larger than the image pixel size, however sub-pixel analysis techniques, such as spectral-unmixing, can be used. In some cases the variation in spectral reflectance due to cover of seagrass can be used as a primary discriminating factor for per-pixel or object-based image classification to produce maps showing ranked classes in terms of "percentage seagrass cover" (Lyons et al. 2013; Roelfsema et al. 2013). For this detailed level of analysis it is even more critical that imagery can provide good a visual signature and differentiation of seagrass. This generally limits its applicability to shallow optical clear locations that contain seagrass community and species types that are relatively large and dense. For some smaller growing species and for locations where water depth and clarity limit this other field based approaches should be considered.

***Approach and algorithms***—A range of approaches are used to estimate these properties, from simple empirical regression models to complex deterministic numerical models, using field data with radiative transfer equations and multi- and hyper-spectral image data sets. In the context of empirical models, field measurements are often made of the seagrass property to be estimated, e.g., above-ground biomass, and these are either related to coincident field spectrometry of the sampled site, or coincident airborne and satellite image data. In either case the field spectrometer and coincident airborne and satellite image data provide at-target reflectance or absorbance measurements of sunlight in selected spectral bands from the location where seagrass property were measured, and can be used to build a regression model between one or more spectral band reflectance measurements and the seagrass property. The modelling results allow a regression equation to be applied to each pixel in an airborne or satellite image to estimate the seagrass property from the reflectance value. Ideally this process uses the same spectral bands and spatial sampling scale to build and apply the model, however this may not be possible.

A second approach for estimating these properties is to use radiative transfer models (Hedley et al. 2005), which estimate reflectance values from known plant structure and physiological parameters, in combination with airborne or satellite images. These models are often run to simulate airborne or satellite measured reflectance under a wide range solar and viewing geometries, water depths and clarities, canopy forms and plant conditions. The results then provide a (look-up) table of possible reflectance values and the seagrass and environmental properties that produced them, allowing the seagrass structure and physiological properties to be estimated for each pixel.

A third approach for estimating percentage cover and biomass does not provide numerical values, as noted above but uses per-pixel or object-based image classification to produce maps showing ranked classes in terms of "percentage seagrass cover or biomass" (Lyons et al. 2013; Roelfsema et al. 2013).

### *15.4.4 Considerations for Mapping and Monitoring Seagrass*

For any desired seagrass map to be generated, the process requires image data to cover the area, and some expert knowledge of the area. The following section outlines critical considerations for all forms of seagrass mapping using the methods outlined in Sects. 15.4.1–15.4.3.

***Mapping of large extents (>$10^3$ km$^2$)***—To create a meaningful map of a large extent is a logistical and physical challenge. Any large body of water has varying water clarity which varies spatially and temporally, due to tidal fluctuations and a range of other factors. The first stage is to assess what mapping method is appropriate for the species/habitat and water conditions—Can remote sensing actually be applied or will you need to rely on more ground based methodologies? The second stage of any mapping project for a large area is to ideally acquire cloud-free and appropriate spatial scale satellite imagery with predominantly clear water at low tide. Using this imagery and any available expert knowledge, potential seagrass locations can be identified.

Once potential locations are identified, a field campaign can be designed to sample a suitable number of locations with seagrass, or at across a range of species types, coverage and biomass levels. The most efficient way to achieve this is to perform spot checks from a boat using waypoints created from the locations identified on the satellite imagery. Spot checks can be done by either a snorkeler, or by drop camera in unsafe waters. As sample locations are visited the snorkeler enters the water and the presence of seagrass, with an estimation of percent cover of the substrate, can be recorded along with its location and depth. It is also useful to record the seagrass species present if known. Photographs taken underwater at each site provide a georeferenced archive which can be used to check other field observations. One caveat for this approach is that snorkeler spot checks are highly dependent on water depth, clarity and the safety of the personnel. In waters deeper than about 3 m, shallow turbid waters, or waters that are known to be unsafe, a drop camera should be employed. In shallow inter-tidal areas with potentially harmful marine life (e.g., crocodiles, sharks, jellyfish) helicopters have also been used to conduct spot check surveys and collect information required at low tide.

***Mapping of smaller extents (<$10^3$ km$^2$)***—If the area to be mapped is relatively small and requires repeat monitoring, spot check or snorkel transects may be used to collect field data If the area is a shallow, coastal area with clear waters, transect data are preferred, from a logistical point of view, however randomised replicates are better than transects in small sites? In this case a snorkeler enters the water and swims from point A to point B taking photographs of the benthos at regular intervals. These photographs can be georeferenced if the snorkeler tows a GPS. On completion of the field campaign, the photographs can be analysed for seagrass presence/absence, percent cover, or species present. Again, snorkeler acquisition of field data must only be undertaken with complete regard to the operational health and safety of the personnel.

*Challenges for mapping seagrass presence and absence using spot check field data*

As for all marine remote sensing applications, mapping the benthos is dependent upon the ability to view the substrate or features you are trying to map on a satellite image. Light is attenuated by water and its constituents, such as sediments, dissolved organic matter, and phytoplankton. Light attenuation makes benthic features in satellite images less visible. Hence, it is generally only possible to accurately map seagrass in areas that are shallow where the waters are clear where seagrass can be differentiated from other bottom types. Seagrass can be mapped in more turbid waters, but the accuracy of these maps is much lower (Roelfsema et al. 2013).

Not only can light availability restrict the ability to map seagrass, but at depth, other benthic features such as algae and coral, may possess similar spectral signatures to seagrasses and look very similar on the satellite image. In this case, maps of seagrass may be rendered less accurate by the inclusion of areas of algae and coral. Acquisition of further spot check data for confirmation of the benthic habitat present can reduce this problem. However it may mean that mapping of seagrass may need to consider to what extent field data can be used to improve mapping, or if only field survey can be done, what is the limited area it can cover. It is important for the end user that any map generated is accompanied by a list of caveats as well as the calculated accuracy of the mapped areas, and a map showing the reliability of field and mapping data.

Some seagrass species differ significantly in their structural form (e.g., leave, strap, cylindrical), cell structure and pigment content, resulting in significantly different spectral signatures, and visually distinct patterns between species (Fyfe 2003). However this may not be the case for all seagrass species, particular some of the tropical species where many may have similar sized strap bladed features, meaning they may be difficult to differentiate. The differences between signatures is also reduced by the effects of epiphytic growth, water depth, water clarity and substrate colour (Fyfe 2003). Figure 15.6 shows the results from a simulation of

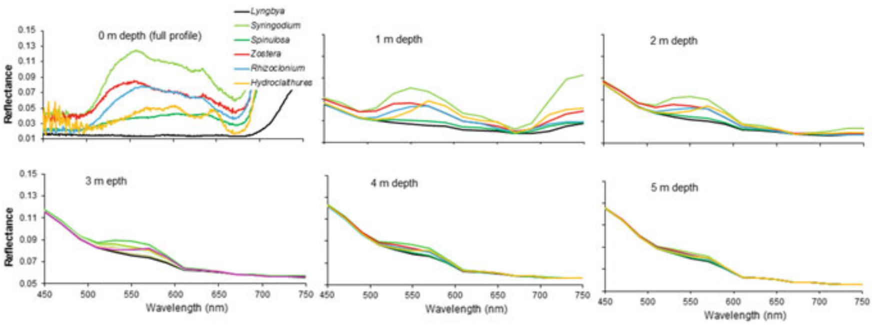


**Fig. 15.6** Modelled seagrass and benthic cover type bottom-spectral reflectance signatures with increasing water depth using optical properties from a clear coastal embayment in eastern Australia. The top left panel shows the exposed spectral reflectance based on field spectrometer measurement of seagrass above the water. The other panels show the modelled at-surface reflectance in the multi-spectral bands of the MERIS sensor, with increasing amounts of water depth

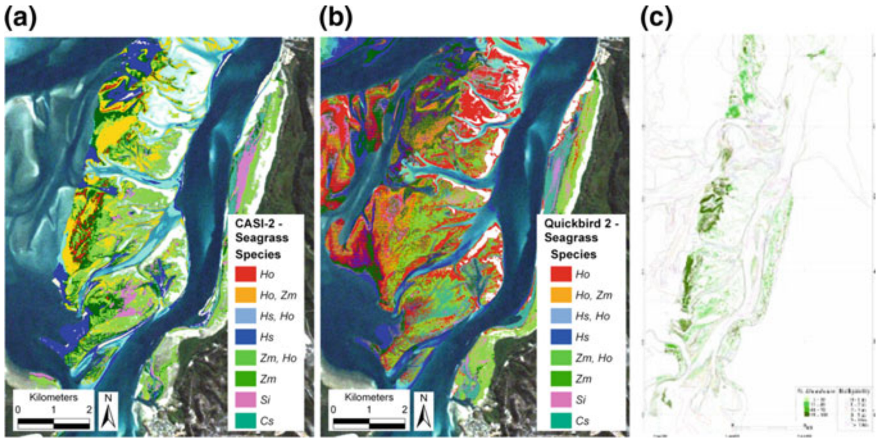


**Fig. 15.7** Seagrass species maps to 3.0 m depth for the Eastern Banks derived from **a**, **c** hyperspectral CASI-2 image (4 m × 4 m pixel size); and **b** multi spectral Quickbird-2 image (2.4 m × 2.4 m pixel size). The seagrass species mapping approach was based for **a** and **b** based on supervised classification, and **c** inverse physics based approach. Seagrass species: Ho—Halophila ovalis, Hs—Halophila spinulosa, Zm—Zostera muelleri, Cs—Cymodocea serrulata and Si—Syringodium isoetifolium (Phinn et al. 2008)

seagrass and algae species spectral reflectance under an increasing range of water depths, with the overall separation between targets decreasing as water depth increases.

Spectral reflectance signatures are often derived using field based measurements 1–10 cm from the subject, so that the field of view of the sensor covers a homogenous part of the subject. Airborne and satellite sensors used for seagrass mapping have pixel sizes 0.1–30 m in size. As explained in Sect. 15.3, for seagrass to be mapped using this approach the seagrass properties must be homogeneous at scales larger than the pixel sizes. Accuracy of mapping is also helped by having more spectral bands, hence hyperspectral imagery is considered more suitable for pixel based approaches. More recently, semi-automated approaches have been developed as well for improving mapping accuracy using high spatial resolution multi spectral imagery (Roelfsema et al. 2014) (Figs. 15.7 and 15.8).

## 15.5 Modelling and Monitoring Seagrass

Seagrasses occur in highly dynamic coastal environments, with their distribution and condition being controlled by a range of environmental factors. This section provides a conceptual basis for using remote sensing to map, monitor and model variability in the seagrass properties discussed in the previous section (presence/absence, type and percentage cover). Concepts from landscape ecology are first

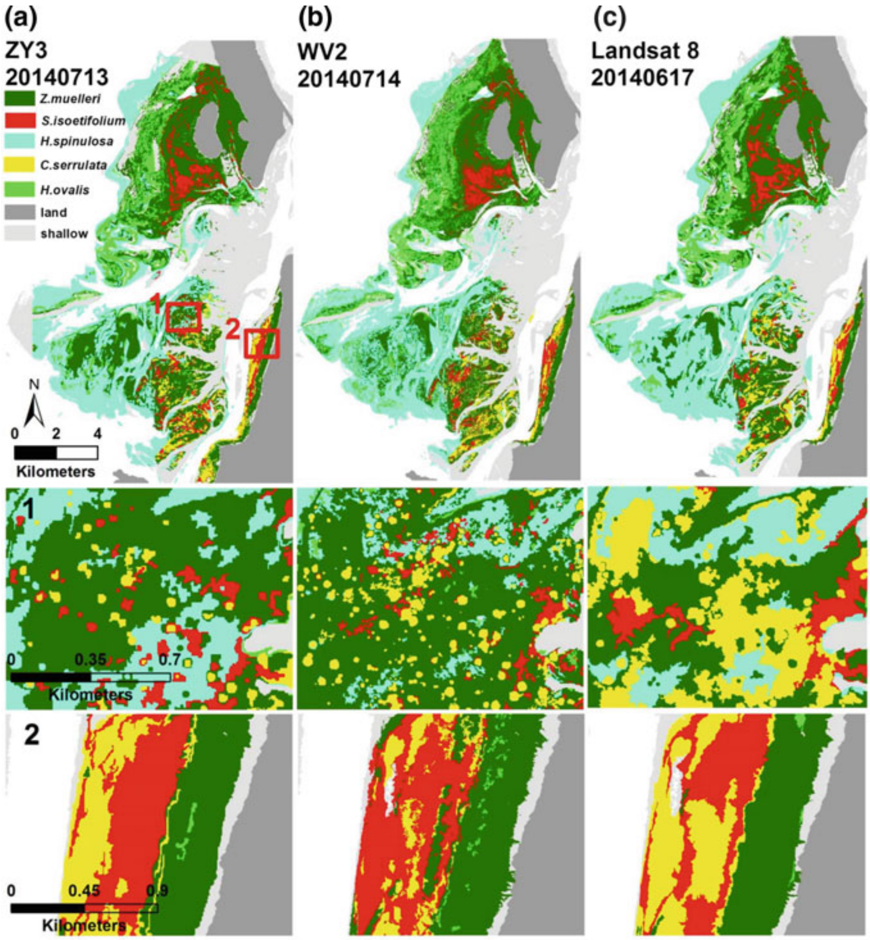


**Fig. 15.8** Seagrass species maps derived using semi-automated object based analysis approach applied to multi spectral imagery with various pixel sizes: ZY3 (5 m × 5 m pixel size) (**a**), Worldview 2 (2 m × 2 m pixel size) (**b**) and Landsat 8 OLI (30 m × 30 m pixel size) (**c**)

used to define seagrasses as seascapes. This provides the basis for outlining multi-temporal analysis techniques to map changes in seagrass, followed by an outline of how seagrass properties and their controlling processes can be modelled.

## *15.5.1 Seagrasses as Dynamic Seascapes*

Seagrass growth dynamics for a given area are driven, in general, by two main factors: seagrass plant properties (physiology and metabolism) and external environmental properties. However in a given area, properties of these two factors can vary spatially and temporally. Thus to understand the mechanism of seagrass distribution changes as a whole, a given study area can be viewed as a "seascape". Seascape is defined similarly to the term "landscape" in landscape ecology, but applied in a marine environment context. Farina (1998) defined landscape ecology as the understanding of the mechanism driving change in landscapes with particular focus on the role of spatial arrangements of pattern and processes. Viewing seagrass areas as seascapes enables understanding the mechanism of change in a seagrass seascape as driven by the spatial arrangement of relevant pattern and processes for both plant properties and the external environment properties. This requires a thorough understanding and measurement of the relevant environmental processes as well as the seagrass measurements.

***Deriving a seagrass seascape structure***—In understanding the spatial and temporal forms of seagrass dynamics, it is helpful to consider it as part of a seascape, in the same way that terrestrial vegetation is part of a landscape. Using the organizational structure of seagrass in the seascape, the basic elements are the following: shoot (also called as clone), patch, meadow (Larkum et al. 2006) (Fig. 15.2). The shoot is the basic unit which has an apical rhizome meristem from which new shoots may develop. Several shoots which are physiologically connected together sharing the same shoot origin is called a "ramet" (Bearlin et al. 1999). The "patch" level originated from landscape ecology studies and is defined as a spatially contiguous group of features sharing a common mapping category (Turner et al. 2001). Similarly the term "bed" is also defined as a spatially contiguous area of seagrass area but the mapping category shared is percentage cover (Robbins and Bell 1994; Lathrop et al. 2006). Meadow in general refers to a study area as a whole but in a spatial context, may be defined as a spatially contiguous seagrass area of varying seagrass percentage cover composition (Lathrop et al. 2006; Robbins and Bell 1994). The following spatial scale associations were set: shoot (centimetre to metre scales), patch level (meter to hundred meter scales) and meadow (hundred meters to kilometres scales).

Taking the three basic seagrass seascape elements and the spatial scale associations, a conceptual model of seagrass seascape structure was created (Fig. 15.2). This model presents the seascape as multilevel, with each level associated to a spatial scale. It also extends beyond the meadow level to represent larger spatial extents, adding the regional meadow level and the ecosystem level. One strength of viewing the seagrass seascape using this model is that it acknowledges: (1) different mechanisms of change may exist at each level; and (2) changes in a level may influence other levels. Obvious linkages are also revealed, as each level is comprised of several "units" from a lower level. For example, the regional meadows level is comprised of individual meadows, meadow level is comprised of patches and patch level is comprised of shoots.

***Seascape physiology and metabolism: Growth at different spatial scales***—Now that a basic seascape structure has been created, understanding changes in the seascape requires: (1) assessing and analysing what drives the changes occurring at each level and/or across levels for a target seagrass variable or property; and

(2) determining the linkage between levels. This leads to a hierarchical approach for understanding seascape change. This approach has been applied successfully in terrestrial environments for linking information at different scale/levels (Wu 1999).

***Seascape biological dynamics: Scaling and mapping***—Studies on seagrass dynamics have focused on either shoot, patch or a meadow covering a range of spatial scales (Figs. 15.9 and 15.10). Viewing seagrass as seascapes means that current knowledge of seagrass dynamics such as spatiotemporal growth need to be put in a seascape context. Placing these in a seascape context requires the process of scaling.

Scaling can be defined as the process of estimating a biophysical variable, ranging from structural (biomass, shoot density, percentage cover) to physiological (photosynthesis, primary production), from the spatial scale of the original measurement to a larger spatial scale. The main challenge in this area now centres on how to account/integrate the contribution of spatial heterogeneity (Turner et al. 2001). The components of the scaling process involve assessing scale characteristics of the scaling problem which comprises of the dimension, kinds and components of scale as shown in (Wu et al. 2006).

*Examples of scaling*:

The scaling process can be divided into two approaches: (1) assume homogeneity (no spatial variation); and (2) assume and incorporate heterogeneity or spatial variation. For example, if total seagrass biomass for a particular seagrass area was to be estimated from field measurements.

The scaling procedure can be applied as follows:

Using the first approach (assume homogeneity), biomass sample measurements can then be taken anywhere within the area to generate an average seagrass biomass per unit area. This “average seagrass biomass per unit area” can then be multiplied to the total seagrass area to produce the total seagrass biomass of the target seagrass area.

Using the second approach (incorporate heterogeneity), the driver(s) of biomass spatial variability need(s) to be identified. Alternatively, another approach is to have enough measurements over the area and through time to provide a reliable estimate of the degree of heterogeneity/spatial variability. Once the driver of spatial variability is identified (i.e., percent cover), biomass sample measurements can then be done for each percent cover level (or range/class). In addition, the amount of seagrass area for each percent cover level or range/class must be determined. Finally the total biomass can be determined as a cumulative sum of the biomass estimated for each percent cover level or range/class. Where biomass for each cover level or class was derived by multiplying the “cover level specific average seagrass biomass per unit area” with the “corresponding cover level seagrass area”.

Such examples of scaling biomass from original scale to target scale is rather a simple one, but the point is, that in most cases, spatial variability exist at all spatial scales. So the first scaling approach (assume homogeneity) in scaling is good as a rough or initial estimate that need to be followed by a robust estimate that incorporates spatial heterogeneity. On the other hand, the second approach (which

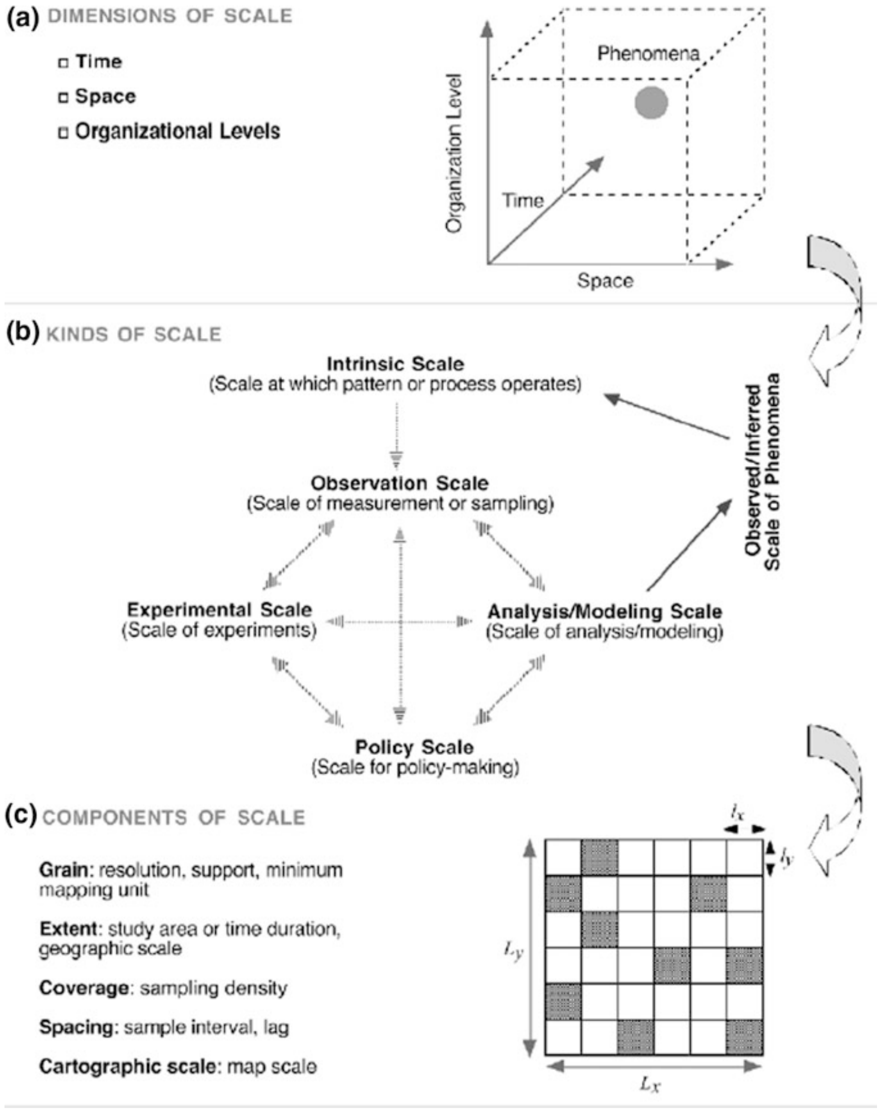


**Fig. 15.9** Hierarchy of scaling concepts showing the different scale characteristics (Figure taken from Wu et al. (2006)

incorporates spatial heterogeneity) may lead to multiple drivers and so the amount of heterogeneity incorporated will depend on the purpose of the estimate.

The approach we have presented above is necessarily simplistic. In reality a good understanding of the spatial (and temporal) variability (or heterogeneity) of the particular seagrass feature being assessed is required to determine the appropriateness of scaling up sub-sampled data to larger spatial scales. It will inform the

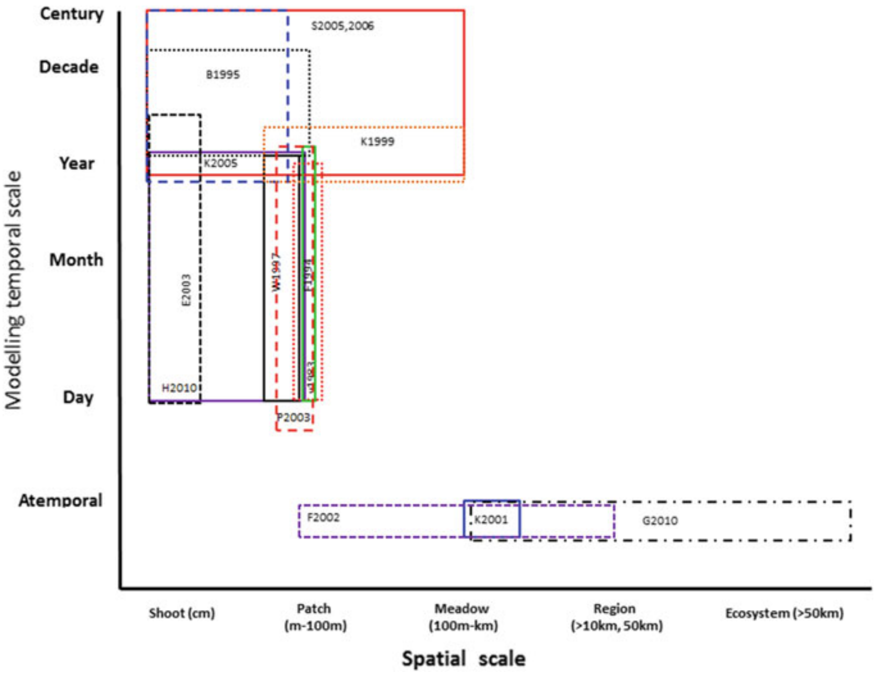


**Fig. 15.10** The temporal and spatial extent of 14 seagrass modelling papers (as individual rectangles), showing limited efforts at meadow to ecosystem scales (Note: atemporal—only modelled spatial variability). The numbers in boxes refer to specific published papers—see Appendix 1

number of sub-samples required to do this reliably and the most appropriate method of obtaining these -random spots throughout or clustered transect data and how many of each for example. We should also note this will not necessarily be the same for all seagrass meadows/landscapes/species/locations. The assumption of homogeneity is also problematic for many seagrass landscapes in Australia—it may well work reasonably for some species and meadows but there are many examples of very large seagrass areas the lack homogeneity and this approach may not be applicable.

### 15.5.2 Mapping and Monitoring Seagrass Dynamics

Remote sensing methods offer a unique opportunity to measure, map and monitor the spatial and temporal dynamics of seagrass ecosystems at a range of scales, but there are several key interactions to be considered between the technology, methodology and biophysical information one wishes to observe. Moreover, there are logistic and financial challenges that may limit monitoring ability at certain

**Table 15.3** Types of biophysical information that can be mapped/monitored as a function of spatial and temporal monitoring requirements—E = extent; C = composition; S = structure; P = physiology

| | | Spatial scale (image pixel size) | | | |
|---|---|---|---|---|---|
| | | Shoots E, C, S, P (<1 m pixels) | Patches E, C, S, P (1–5 m pixels) | Meadows E, S[a] (5–30 m pixels) | Regional E[a] (30+ m pixels) |
| Monitoring frequency | Daily | $$$ | $$$ | $$$ | $ |
| | Weekly | $$$ | $$ | $$ | $ |
| | Monthly | $$ | $ | $ | $ |
| | Annually | $ | $ | $ | $ |

$—Cheap, routine, operational

$$—Expensive, but feasible

$$$—Generally infeasible due to either monetary or resource requirements

[a] Accuracy of such a product would need to be carefully considered, with a higher risk of errors described in Table 15.4

spatial and temporal resolutions (Roelfsema et al. 2013). In this section we first broadly classify the types of biophysical information that can be monitored as a function of spatial and temporal monitoring requirements, and the requirements for conducting reliable and accurate assessments of changes in seagrass properties over time (Tables 15.3 and 15.4). We note while that much of this section may apply to change detection over a two to three dates of seagrass maps, monitoring seagrass dynamics typically requires a time series of at least five maps (Lyons et al. 2013; Roelfsema et al. 2014).

Extent is the most simple seagrass property to map, and naturally has the oldest records of maps derived from remote sensing techniques in Moreton Bay (Hyland et al. 1989; Young and Kirkman 1975). However, this ease of mapping typically results in these records being derived from a range of image sources and mapping methodologies. For example even in Moreton Bay, one of the most extensively mapped seagrass regions in the world (Dennison and Abal 1999; Hyland et al. 1989; Roelfsema et al. 2009, 2014; Young and Kirkman 1975), the time series of seagrass extent maps was not reliable enough for a quantitative assessment of change (Roelfsema et al. 2014). This was due to irreconcilable differences in survey techniques and mapping methods. In smaller study areas however (e.g., Eastern Banks—Lyons et al. 2013; Roelfsema et al. 2014), quantitative assessment was possible for seagrass time series derived using equivalent mapping methods (Fig. 15.11). Chapter 9 on Seagrass seascape dynamics presents a case study applying remote sensing change detection techniques to Moreton Bay, Queensland Australia.

**Table 15.4** Requirements for conducting reliable and accurate assessments of changes in seagrass properties over time using remote sensed data Roelfsema et al. (2014)

| Data/product requirements | Possible errors | Example error impacts |
|---|---|---|
| *Spatial characteristics* | | |
| Georeferenced | Misaligned maps | False positive change detection |
| Equivalent spatial extent | Missing data | Areas not mapped at all dates falsely detected as change |
| Equivalent mapping categories | Incomparable map categories | Detected changes represent change in mapping category instead of real change |
| Equivalent spatial resolution | Minimum level of detail mapable | Small patches of seagrass detected in some maps but not others |
| *Temporal characteristics* | | |
| Sufficient temporal resolution (∼5 + time stamps) | – | Unable to establish pattern or causes of detected seagrass changes |
| Seasonal sampling | Natural variation | Decline or increase in seagrass detected due to seasonal differences |
| Similar hydrodynamic conditions (tide, water clarity) | Ability to detect seagrass through water column | Higher tide or turbid water results in reduced chances of detecting seagrass |
| *Mapping methodology* | | |
| Reproducible mapping method | Variation in methodology | Detected changes due to errors in methodology replication instead of real change |
| Replicate field samples | High variance in calibration/validation data between maps | Detected changes due to variance in field data instead of real change |
| Sampling accuracy | Decreased reliability | High variance in mapping accuracy between dates |

### 15.5.3 Mapping Physical Factors Influencing Seagrass Dynamics

The previous section discussed two options for scaling up seagrass distribution outside of sampled areas. The second of these methods requires data on the spatial variability in abiotic and biotic variables. This is possible because the distribution of seagrass habitats is determined by abiotic and biotic factors. Creating predictive maps of seagrass distribution using models therefore requires knowledge of the spatial distribution of those factors. This section focuses on how maps of some of the physical factors influencing seagrass are generated. Biotic factors such as competition or disease also influence seagrass distribution but are not the focus of this section.

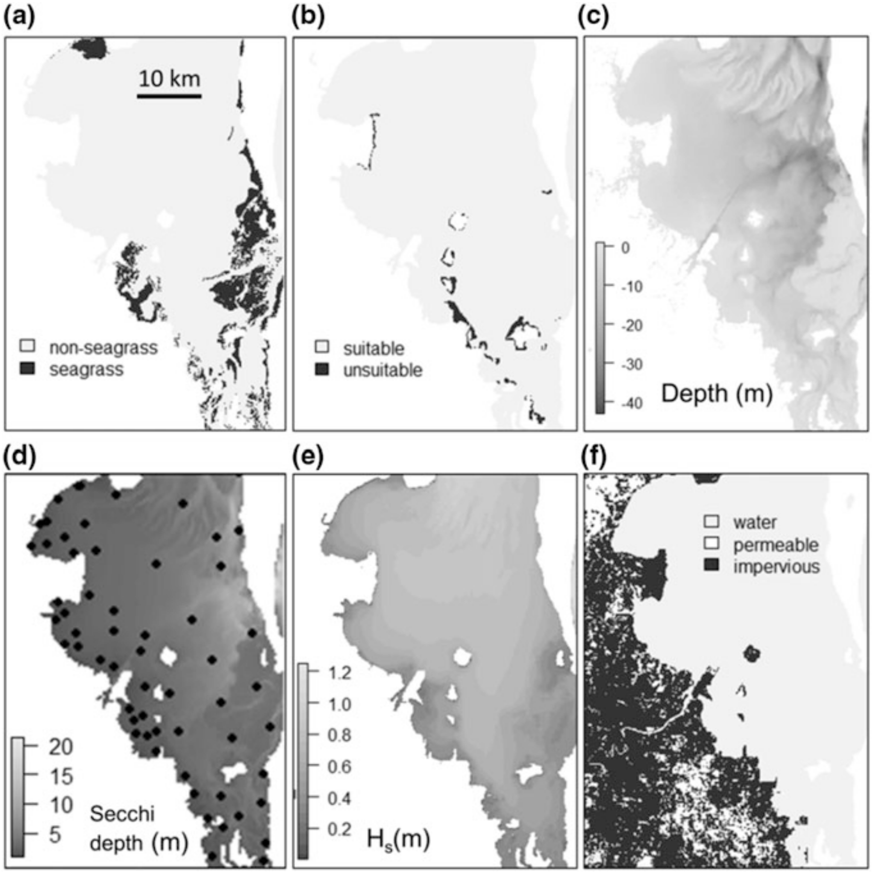


**Fig. 15.11** Data used to model seagrass presence versus absence in Moreton Bay, Southeast Queensland, Australia. **a** Seagrass versus non-seagrass marine habitats (Roelfsema et al. 2009). **b** Suitable (sand, mud) versus unsuitable (rock, coral) substrate (from former DERM, now DSITIA). **c** Digital terrain model (+1 to −40 m shown). **d** Water clarity: secchi depth (m), modelled using data obtained from sampling sites indicated by points (see Table S1). **e** Significant wave height (Callaghan et al. 2015). **f** Presence of impervious surfaces at 30 m resolution derived from landsat imagery in Moreton Bay, Southeast Queensland, derived from Lyons et al. (2011). [Quoted directly from Saunders et al. (2013)]

Physical environmental data are very important for modelling seagrass distribution, abundance and function. Water depth, water clarity, photic depth, water temperature, currents, waves, and tidal range all influence seagrass properties (Adams et al. 2015; Callaghan et al. 2015; Carr et al. 2010, 2011, 2012; Grech and Coles 2010; Koch 2001; Koch et al. 2006; Saunders et al. 2013, 2014). Minimum water depth for seagrass occurrence is primarily determined by wave orbital velocity, tide and wave energy producing exposure related stress, whereas maximum depth is determined by light availability (de Boer 2007). For spatial models of seagrass distribution to be produced spatial data sets of physical environmental data are typically required. The types of data required are context dependent, and will vary based on the spatial scale of the study, environmental setting, and purpose of the model. A first step in the modelling process is identifying the most important physical environmental data for the scope of the study identifying biases which may be introduced by omitting other factors.

Spatial variability can be dealt with by setting spatial resolution and extent to that of the coarsest resolution and smallest range of the data available, or by making estimates of unknown values in un-sampled regions using models. Physical environmental data vary spatially and temporally in the coastal zone.

Where large data sets are required, for practical purposes, decisions must be made about reducing data sets to a size which is tractable, yet still represents the spatial and temporal variability in environmental data in a meaningful sense.

Ideally, environmental data would be available for each location for which seagrass presence or abundance were being modelled (Fig. 15.11). However, in reality this is often not the case, particularly for large or remote study areas. Alternatively, input data for models of seagrass distribution may be either measured at point locations and extrapolated to un-sampled locations if necessary, or modelled. The following sections give examples of how data sets for some of the important variables influencing seagrass distribution have been derived.

***Bathymetry***—Water depth influences seagrass distribution primarily by affecting the availability of light on the seafloor and the influence of waves and tidal currents on the benthos. Maps of bathymetry can be obtained from bathymetric charts, which are typically derived from ship soundings (Beaman 2010), or by remote sensing imagery informed by field data (Leon 2012).

***Water clarity***—Water clarity can be estimated from remote sensing imagery in optically deep water (that is, in locations where the satellite cannot “see” the bottom). However, seagrass can only live in optically shallow water where light is sufficient to support photosynthesis. Therefore, remote sensing is not typically used for deriving maps of water clarity in regions occupied by seagrass (Phinn et al. 2005). Instead, data for water clarity is obtained from field sampling. In Moreton Bay, QLD, secchi depth was based on field data obtained at point locations sampled monthly in July 2003-2004 from the Ecosystem Health Monitoring Program (EHMP) (Adams et al. 2015; Callaghan et al. 2015; Saunders et al. 2013). The point data for water clarity were extrapolated to un-sampled locations using a simple linear model based on distance to rivers (a source of turbid water) and open ocean (a source of clear water) (Saunders et al. 2013).

***Benthic light availability***—Benthic light availability is a function of water clarity, water depth, and surface irradiance. Given data on water depth and water clarity, benthic light availability can be calculated as a percentage of the light available at the surface. In general seagrass require 10% of surface light (Duarte 1991) although some species can survive with less and this requirement is now known to vary significantly between species (Collier et al. 2012). It can also be measured in situ using PAR loggers as light reaching the seagrass canopy.

Temporal variability in benthic light availability has been simplified to model seagrass distribution by averaging over monthly or annual time scales (Saunders et al. 2013, 2014). However this method could omit important information, such as the duration of time that low light conditions affect plants. Several authors (Adams et al. 2015; O'Brien et al. 2011) addressed this issue by deriving and testing the explanatory power of multiple indicators for the light affecting seagrass plants. These indicators included mean annual benthic light dose at the seabed, mean annual light penetration, the number of months in the year with mean benthic light dose less than 10, 15 or 20% of the mean annual surface light dose, and the number of months with light penetration less than 10, 15 or 20%. Each variable was then used in independent species distribution models of seagrass presence, and the best performing variable was selected based on Akaike Information Criterion (AIC).

***Water temperature***—Seawater temperature affects the community structure of seagrass habitats. Seawater temperature is measured in situ using temperature logging instruments moored at point locations, instruments located on moving objects such as vessels, or from satellite imagery using remote sensing. The latter can only measure the temperature at the sea surface, which may vary significantly compared to temperature at depth. Maps of seawater temperature may also be derived from oceanographic models. For a model of seagrass distribution in the Great Barrier Reef, mean sea surface temperature in the Australian region were obtained from the Australian Commonwealth Scientific and Research Organisation (Grech and Coles 2010).

***Currents and wave***—Waves and currents are measured at point locations in coastal areas using wave buoys and current meters. These instruments are costly and in most instances only have limited spatial coverage. Maps of wave heights and currents may be derived from oceanographic models. In Moreton Bay QLD, and at Lizard Island QLD, wave heights were modelled using the Simulating WAves Nearshore (SWAN model) (Callaghan et al. 2015). Similarly, March et al. (2013) used a wave model to generate data for wave orbital velocity, significant wave height, and peak period, which were used to model *Posidonia oceanica* distribution at Palma Bay, NW Mediterranean. However, such relatively complex process based wave models are not always accessible to ecologists. Simpler "fetch-based" approaches to generating maps of wave properties can be used, albeit with limitations (Callaghan et al. 2015).

***Tidal range***—Tidal range affects the distribution of seagrass over relatively large scales, such as over the extent of the Great Barrier Reef (Grech and Coles 2010). Tidal range data may be obtained from published maps. For instance, tidal range data from Hopley et al. (2007) were used to model seagrass presence or absence in the Great Barrier Reef by Grech and Coles (2010).

***Substrate type and sediment composition***—Most seagrass species require soft sediment substrates (with the exception of the surfgrasses, *Phyllospadix* spp. and *Thalassodendron cilliatum*—tropical Australian species that can grow on rocks/reefs directly) with a preference for medium grained sediments. Maps of substrate type and sediment composition are derived by remote sensing, echo-sounding, or by analysing sediments from sediment grabs or cores. In Moreton Bay Australia, a map of mud concentration (% mud) was derived by interpolating among data points obtained from sediment cores (Adams et al. 2015). Based on this map, maps of the time for 50 and 90% of sediment to settle over a depth of one metre were derived.

## 15.6 Monitoring and Managing Seagrass?

Seagrass habitats globally are threatened by anthropogenic and natural impacts necessitating active monitoring and management (Orth et al. 2006; Waycott et al. 2009). Mapping the distribution of key habitat forming species is often one of the first priorities for monitoring programs to ensure that informed ecosystem based management decisions are made (Cogan et al. 2009). Habitat mapping via remote sensing is important for environmental management as it has the potential to provide data at spatial and temporal scales that are relevant for management, and enables field based measurements to be extended over larger areas and longer time periods (Stevens and Connolly 2004). For habitat mapping to be successfully integrated into environmental decision-making, however, it needs to be available to practitioners in a useable context, in terms of data form and supporting information, that provides relevant information to understand the variability of a system (Benson and Garmestani 2011).

Environmental managers are beginning to account for ecological complexity into management planning strategies, with the understanding that ecosystems are rarely in a state of equilibrium, rather they are complex systems that vary with changing internal and external pressures (Gunderson et al. 2009). As this understanding grows, the habitat mapping technologies based on for instance remote sensing must grow with it in order to continue to deliver information relevant for decision-making.

### *15.6.1 Requirements for Remote Sensing to Be Used by Seagrass Managers*

The increase in accessibility of high spatial resolution imagery and free satellite imagery has increased our ability to create seagrass habitat maps at various spatial scales and extents (Roelfsema et al. 2013). However, it remains important that a clear understanding of what this imagery is capable of delivering and its limitations accompanies attempts at mapping and monitoring assessments and that appropriate methods for the physical and biological nature of the seagrass communities are applied. It is now no longer enough, however, to provide maps that solely describe the extent of seagrass. This is largely because the prevention the loss of seagrass at the landscape scale requires managers to track additional indicators that provide prior warning of that loss (van der Heide et al. 2008). By the time that seagrass decline is depicted in habitat mapping products at the landscape scale, it is often too late to respond (Hughes et al. 2010). Additionally, with an increase in the understanding of the stressors on seagrass meadows, managers now require habitat maps that allow them to decipher trends in seagrass condition and to correlate that condition with variation in stressors at the same spatial and temporal scale. Managers often have two key requirements: (1) to identify seagrass areas at most risk and therefore greater need for protection; and (2) to identify the effectiveness of the management actions taken to protect or restore meadows. As such seagrass distribution (extent and composition maps) is only one of the information types that managers now require from remotely sensed seagrass habitat maps. Recent improvements in remote sensing capabilities have begun to allow the development of the additional elements required for managers to better understand the variability of their system.

### *15.6.2 Mapping at Scales Relevant to Management*

The biophysical properties of seagrass meadows have been well studied at the cellular, physiological, morphological and meadow scales, however there has been limited demonstration linking the temporal dynamics of biophysical characteristics at those scales to temporal changes at the sea/landscape scale (Kendrick et al. 2005). Longer term datasets (>10 years) based on plot or transect measurements, often lack the coverage in terms of spatial extent required to make broader scale ($km^2$ seagrass meadow and above, Fig. 15.2) assessments of seagrass dynamics (Lyons et al. 2013). Providing detailed information at relevant spatial or temporal scales has always been a limiting factor for seagrass management). In many monitoring programs there exists a juxtaposition between the requirements for very detailed information at fine resolution (e.g., patch—meadow scales Fig. 15.2) for location scale planning across very large spatial extents (ecosystem scale, Fig. 15.2) despite very minimal financial resources. These requirements have become prerequisites for managers in the course of planning and maintaining coastal infrastructure (e.g., harbours, piers, coastal protection, dredging of waterways) while still ensuring the conservation of regional ecosystem function and values. While concepts of landscape ecology are becoming more widely used and tested in seagrass empirical studies (Boström et al. 2006), baseline, longer term datasets describing the patchiness or fragmentation have been elusive.

Recent techniques like object-based analysis have proved useful in providing large spatial scale assessments with finer resolution (Lyons et al. 2012). Applying these sorts of techniques to coarse proxies for seagrass condition like percent cover has provided managers with a greater understanding of temporal seagrass dynamics at larger spatial scales.

### *15.6.3 Requirements for Understanding Processes*

Remote sensing can provide managers with a better understanding of how naturally transitory seagrass meadows compare to more enduring meadows. Transitory meadows are not persistent over time; with periods of seagrass absence interspersed with periods of seagrass presence. Well-known examples of transitory seagrass ecosystems are seasonal meadows that develop from the seed bank, grow, flower and die each year, and they are meadows that do not lend themselves to using remotely sensed satellite or airborne imagery analysis, including small *Halophila* species and/or deepwater species (Kenworthy 2000; Meling-López and Ibarra-Obando 1999). The difficulty for managers is to separate meadows that are naturally transitory from those that fluctuate in response to fluctuations in stressors. Understanding how changes in stressor levels correlate to the fluctuations of meadow condition requires the provision of data at the same spatial and temporal scales.

## 15.7 The Challenges and Future for Seagrass Remote Sensing

The earlier sections of this chapter demonstrate operational methods for choosing and combining field and remotely sensed data to map and monitor seagrass environments at a range of specific scales and for deriving specific map products that are directly relevant to scientific and management questions. There are still a number of challenges to be addressed, partly in relation to advances in our capabilities to acquire and process data. The following section outlines the main challenges and potential directions for addressing these.

There are four main challenges which we will continue to address in using remote sensing to map seagrass environments:

(1) Selecting the most appropriate image data set(s) and mapping algorithm(s) to use for specified seagrass properties;
(2) Producing map products that are ecologically appropriate and suitably accurate;
(3) Measuring and presenting the accuracy properly for maps of seagrass properties; and
(4) Re-inventing or duplicating existing methods.

The first two challenges are a function of the continual increase in the range of airborne and satellite imaging systems being made available for private and public use, which is accompanied by a shift towards open access data and image processing software. The net result of these changes is that remotely sensed data are incredibly easy to access and to process for a much wider range of people. As a result it is easy to obtain an image and attempt to process it, without any expert knowledge or experience with the feature being mapped. The literature clearly shows it is essential for all forms of seagrass mapping to incorporate field data and expert knowledge in the initial selection of the appropriateness of remote sensing for the mapping situation and in the calibration and validation phases of any mapping project. We encourage readers to follow the mapping examples presented in Sects. 15.4 and 15.5 of this chapter. Measurement of thematic map accuracy, for seagrass species composition, or estimation accuracy for seagrass biomass mapping requires carefully designed field programs and use of appropriate error metrics, such as those explained in Sect. 15.3. However, this step is often ignored, or not conducted with sufficient data or appropriate methods, which makes the data un-useable or unable to be compared to other data or to detect changes over time. Building on previous works also ensures the potential for duplication of the work is minimised and enables a shared body of knowledge to be built that will more effectively link ecological and management applications to appropriate remote sensing data collection and processing.

The future capabilities for using remote sensing to map and monitor seagrass and its biophysical properties are extremely promising due to the challenges listed above, including: the greater range of image data sources and processing tools, more open access and shared data and algorithms, and greater ecological-remote sensing interactions. Collectively it means we have a greater data collection and informed processing capacity, that is more likely to share knowledge and skills about how to effectively map and monitor seagrass properties and advance our abilities. It means we can build approaches to work across a range of environments and conditions. A central part of this capacity is improved communication and cooperation and to achieve this a toolkit for explaining how to use remote sensing to map and monitor specific environmental properties, including seagrass has been established—see (Roelfsema et al. 2010) www.rsrc.org.au/rstoolkit—this provides a site for finding data and solutions for mapping seagrass environments.

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# Part VI
# Fauna

# Chapter 16
# The Role of Consumers in Structuring Seagrass Communities: Direct and Indirect Mechanisms

**Robert J. Nowicki, James W. Fourqurean and Michael R. Heithaus**

**Abstract** Seagrass ecosystems were traditionally assumed to be structured by competition as well as by “bottom up forces” such as resource availability and disturbance. However, a wealth of new evidence demonstrates that exertion of “top down control” by animals may be widespread. The strength and direction of top down control is context dependent, however, and varies with properties of organisms, the community, and the physical environment. Consumers can facilitate, consume, or destroy primary producers, aid or inhibit seagrass reproduction, or alter bottom up processes with implications for the properties and persistence of seagrass ecosystems. Studies in Australian ecosystems have been critical in helping to elucidate the role of consumers in seagrass ecosystems. Specifically, work investigating the roles of megaherbivores and apex predators and the pioneering of novel experimental approaches which allow for cage-free manipulations of mesograzers have substantially furthered our understanding of top-down control. At the broadest scale, megagrazers are likely to dominate grazing pathways in Australian tropical and subtropical seagrass ecosystems, while macrograzers and mesograzers do so in

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temperate seagrass ecosystems. However, while we have learned much about mechanisms through which top-down control can operate and its effects on seagrass ecosystems, predicting which grazing pathways dominate at smaller spatial scales, and net herbivore effects on seagrasses in specific ecosystems remains challenging due to context dependence and the highly complex nature of species interactions. Anthropogenic impacts further complicate these relationships. Australian seagrass habitats possess unusual properties, including relatively intact populations of megafauna, remote and pristine locations, and distinctive oceanographic features which allow these habitats to provide unique insights of top down control in seagrass ecosystems.

## 16.1 The Development of Understanding of Top-Down Control on Seagrass Community Structure

One of the central goals of ecology is to understand the forces that structure ecosystems. In pursuing this goal, ecologists have traditionally focused on the roles of physical factors such as light, water and nutrient availability in controlling ecosystems from the "bottom up." This focus on bottom up control was due in part to the ease with which physical variables can be manipulated in controlled experiments. Though ecologists and naturalists had written about the importance of consumers and "top down" forces in ecosystems throughout the field's history (e.g. Elton 1927), it wasn't until a seminal paper published by Hairston et al. (1960) that the role of consumers was brought into the ecological limelight. This paper presented what is known as the "green world hypothesis," and asked a simple question: if herbivores are only limited by resources, then why do plants in terrestrial ecosystems persist? One reason, the authors posited, is that herbivores are not limited from the "bottom up" by plant resources, but from the "top down" by predators—and that this top down control is what allows primary producers to survive. This hypothesis, though remaining far from universally accepted (see Ehrlich and Raven 1964; Murdoch 1966; Strong 1992; Polis and Strong 1996; Polis 1999 for critiques and alternate hypotheses), set the stage for subsequent studies investigating the role of top down control in ecosystems.

Until relatively recently, the importance of top-down control in seagrass ecosystems went largely unrecognized. Indeed, seagrass ecology focused on factors in the physical environment that limited seagrass establishment, growth and distribution—herbivory and predation were considered relatively unimportant (Kirkman and Reid 1979; Klumpp et al 1989). This view began to incrementally change, particularly in the 1980s, when several reviews suggested that the persistence of seagrass ecosystems may be due to herbivore control of algal competitors, which are generally faster growing than seagrasses (Orth and Van Montfrans 1984; van Montfrans et al. 1984). The suggestion that top down control may be important in limiting algal overtake of seagrass ecosystems has since been widely recognized (e.g. Hughes et al. 2004; Heck and Valentine 2007; Verhoeven et al. 2012).

Though there was increasing realization that top down control could play important roles in seagrass-algae dynamics, the paradigm remained that seagrasses *themselves* were only rarely consumed by herbivores and that most seagrass production was probably channeled into the detrital cycle (Kirkman and Reid 1979; Thayer et al. 1984; Klumpp et al 1989). This idea persisted despite the knowledge that sirenians, sea turtles, teleosts and sea urchins that live in seagrass meadows are herbivorous (Klumpp et al. 1989; Lanyon et al. 1989) and that the effects of grazers on the structure of seagrass beds can, in some cases, be readily apparent (Randall 1965). Contributions from historical ecology and contemporary experiments performed over several decades, began to challenge this paradigm.

Taking a historical perspective, some ecologists observed that the seagrass ecosystems of today are rarely intact or natural ecosystems. Modern seagrass ecosystems, they argued, are largely released from top-down control because the marine megaherbivores that roamed such ecosystems centuries or millennia prior had been hunted to functional extinction (Dayton et al. 1995; Domning 2001; Jackson 2001; Heck and Valentine 2007). In a way, this argument echoed that of Hairston et al. (1960)—seagrass ecosystems were green because predators (in this case, humans) were highly effective at exerting top down control on seagrass herbivores such as sea turtles, sirenians, sharks. Thus, ecologist's observations of low rates of herbivory in seagrass ecosystems could in fact be the result of human activity that set an unnatural "baseline" that betrays the truth of the evolutionary and ecological importance of herbivory in these systems.

Other ecologists argued that seagrass herbivory was not only still occurring, but that it could still have strong effects in seagrass ecosystems today. Largely led by the work of ecologists working in the Gulf of Mexico and Northwestern Atlantic, a suite of observations, experiments, reviews, and meta-analyses has built compelling evidence that significant seagrass consumption (and top-down control) continues in contemporary seagrass ecosystems (Valentine and Heck 1991, 1999; Heck and Valentine 1995; Cebrián and Duarte 1998; Rose et al. 1999; Williams and Heck 2001; Kirsch et al. 2002; Hughes et al. 2004; Nakaoka 2005; Valentine and Duffy 2006; Heck and Valentine 2007). Even in the relative absence of marine megafauna, multiple experiments showed how consumer control can still shape seagrass ecosystems at scales from individual plants to the entire community. Partially as a consequence of these and other experiments, the idea that predators play critical roles in controlling herbivory in seagrass ecosystems also gained support (Heck et al. 2000; Williams and Heck 2001; Valentine and Duffy 2006)—something first observed to be important to the formation of the grazing halos described decades before (Randall 1965). Evidence for top down control in seagrass ecosystems (including trophic cascades) continues to accumulate today (Hughes et al. 2004; Burkepile and Hay 2006; Heck and Valentine 2006; Heithaus et al. 2012; Burkholder et al. 2013; Duffy et al. 2013).

By the late 1980s, when the first edition of this book was published, it had begun to become apparent that seagrass herbivory was more important than previously recognized, though most of the focus remained on large bodied consumers like dugongs and green turtles (Lanyon et al. 1989). Now, there is compelling evidence that consumers of varied body size and feeding guild can exert top down control through a variety of mechanism and trophic pathways, sometimes with strong and counterintuitive effects on their ecosystems. The challenge now is not in determining *if* top-down control exists in seagrass ecosystems, but when it is important relative to other forces, by what mechanisms top-down control most commonly operates, and by what pathways it is most likely to dominate. While work to identify mechanisms of top down control has been fruitful, predicting when (and through what avenues) top down control dominates in seagrass ecosystems has proven difficult and remains a key challenge in seagrass ecology.

## 16.2 The Nature of Top Down Control and the Prevalence of Context Dependence

In order to understand when, where, through which pathways and mechanisms, and how strong top-down influences are, an understanding of the roles of consumers, producers, and their relationships to each other and their environment is necessary. In the most basic sense, the strength and nature of top down control in seagrass ecosystems is a function of the properties of herbivores, predators, and the seagrass, community structure, and features of the physical environment. Seagrasses, and the other primary producers they interact with, have inherently different life histories, chemical compositions, and tolerances to herbivory and environmental conditions. These properties interact with properties of herbivores—their densities, identity, consumption rates, or feeding preferences. Predators in turn influence herbivores or the predators of herbivores—altering their density, traits and behavior—which can generate cascading effects to seagrasses. The strength of these interactions is often linked to food web complexity. Consumers also interact with seagrass directly through nutrient transport and concentration, physical restructuring of habitat, and changes to bottom-up processes. Finally, these interactions occur in the context of the physical environment and are further complicated by anthropogenic impacts such as nutrient pollution, predator removal, and climate change. Below we consider how each of these taxa, guilds, or factors influences the strength and nature of top-down control, providing examples from experiments or observational work to support these considerations.

### *16.2.1 The Role of Seagrass in Mediating the Strength of Top-Down Processes*

Plants are not simply the recipients of consumer effects; they also play an important role in mediating the ultimate effects consumers have on the primary producer community. As one ecologist wrote, “Plants are not passive agents, waiting to be decimated by herbivores" (Polis 1999). Primary producers, including seagrasses, microalgae, and macroalgae, can alter the strength of top down control through their susceptibility and response to herbivory, which may, in turn affect herbivore behavior. Seagrasses exposed to herbivory may decline or die-off, exhibit tolerance through compensatory or super-compensatory growth, or display resistance by altering their physiology or chemistry through methods such as nutrient or carbohydrate re-routing or by producing secondary metabolites (Cebrián et al. 1998; Ricklefs and Miller 1999; Vergés et al. 2008; Burnell et al. 2013a; Steele and Valentine 2015). The tolerance of primary producers to different kinds of herbivory differs by species—though it can also be induced in response to herbivory (e.g. Burnell et al. 2013a; Sanmart et al. 2014)—and this differential tolerance can have implications for seagrass community composition. For example, in mixed species seagrass meadows in Lady Bay, South Australia, overgrazing of seagrasses by sea urchins disproportionately impact *Amphibolis antarctica* compared to *Posidonia* spp., because the leaf cluster meristems of *A. antarctica* are exposed at the surface and therefore are more vulnerable to grazing while the meristems of *Posidonia* species are protected beneath the sediment surface (Burnell et al. 2013a). In this sense, differences in morphology mediate the strength of consumer control of these mixed-species beds.

In general, the life history characteristics of pioneer seagrasses like those in the genera *Halophila*, *Halodule*, *Syringodium*, allow them to grow and expand quickly, giving them generally high grazing tolerance on the level of the meadow, even if their standing biomass is often heavily reduced by regular grazing (e.g. Preen 1995; Masini et al. 2001). Climax seagrasses like those in the Australian genera *Amphibolis*, *Posidonia*, and *Zostera* grow and expand more slowly, but are also less ephemeral, forming dense, thick beds with generally higher stocks of standing biomass. This "climax" life history, however, results in slower responses to large grazing events that can be generated by herbivores like dugongs and urchins (see Preen 1995; Eklöf et al. 2008 for examples). Some climax species, like *Amphibolis antarctica*, do not even generate seeds (Hemminga and Duarte 2000), produce viviparous seedlings to recolonize heavily grazed areas. As we will see, life history characteristics also relate to herbivore feeding preferences.

While primary producers alter how top-down control operates in seagrass ecosystems via their responses to herbivory, they also do so through their properties as a resource. Because seagrasses can act as a different kind of resource (i.e. food, shelter) for different consumers, seagrass properties can influence not only herbivore feeding rates and food preferences, but also habitat use preferences. These preferences can have measurable impacts on seagrass community structure (Preen 1995; Armitage and Fourqurean 2006). Consumer feeding patterns are influenced by variation in primary producer chemical properties (i.e. palatability or food quality), structural properties (i.e. complexity, which provides refuge for predators or herbivores), or through community composition (associations with other producers that may illicit such preferences in herbivores).

From an herbivory perspective, seagrass chemical composition describes the concentration of not only nutrients and soluble carbohydrates which often attract grazing, but also fiber and secondary metabolites, which can deter it. Generalizing the relationship between the seagrass chemical composition and herbivore feeding preference or feeding rate remains surprisingly difficult. For example, some studies find a positive relationship between nutrient content and herbivore feeding preference or consumption rates (ex. McGlathery 1995; Brand-Gardner et al. 1999; Goecker et al. 2005; Prado et al. 2010; Sheppard et al. 2010; Burkholder et al. 2012), while others do not (Cebrián and Duarte 1998; Mariani and Alcoverro 1999; Valentine and Heck 2001; Kirsch et al. 2002; White et al. 2011). This is partially due to the fact that nutrient concentrations as measured in assays may not accurately reflect the actual nutritional content a seagrass presents to herbivores since many nutrients can be bound to indigestible plant tissue that is never assimilated (Cebrián and Duarte 1998). However, some of this complexity is derived from simultaneous variation in defensive compounds which reduce palatability. For example, feeding trials and manipulations using the bucktooth parrotfish *Sparisoma radians* indicate this herbivore prefers macrophytes in inverse relation to their terpene content, even when other factors such as species or biteability are accounted for (Targett et al. 1986). Similarly, in Watamu National Marine Park, Kenya, feeding preferences of the teleost herbivore *Calotomus carolinus* are inversely correlated to the carbon fiber content of primary producer species (Mariani and Alcoverro 1999, Table 16.1). The relationship between nutrient ratios, plant defenses, and herbivore feeding preference is further obscured by the fact that plant characteristics can fluctuate across space, time, species, and individual (e.g. Fourqurean et al. 2005; Hays 2005; Tomas et al. 2011; Steele and Valentine 2015). This complicates drawing patterns because multiple chemical variables can change concurrently, making attribution of herbivory to a single compound or group of compounds difficult. For example, newer seagrass leaves generally have higher nutrient concentrations and fewer structural compounds than older leaves, but may also have higher concentrations of phenolic compounds (Hemminga and Duarte 2000; Agostini et al. 1998; Vergés et al. 2010). Older leaves also tend to have higher epiphyte loads, making them more attractive to grazers targeting epiphytes (Alcoverro et al. 1997; Wressnig and Booth 2007; Vergés et al. 2010), and seagrass leaves have higher N and P content in winter compared to summer in seasonal environments (Fourqurean et al. 1997, 2005, 2007). Finally, different herbivores place varying levels of importance on each of these seagrass qualities (Prado and Heck 2011) meaning that understanding herbivore feeding preference requires not only comprehensive knowledge of seagrass chemical properties, but also insight into which of those properties local herbivores consider most. Despite the complex relationship between chemical properties and herbivory, investigations into a generalizable pattern are important as these chemical properties can significantly influence herbivory rates (e.g. Steele and Valentine 2015).

Though the multitude of factors driving herbivore feeding preferences in seagrass meadows has made generalizing preferences very difficult, one general pattern has emerged. Feeding assays, gut content analysis, and herbivore exclosure experiments indicate that faster growing seagrass species—many of which are of tropical origin—are generally consumed more readily than slower growing climax species (Cebrián and Duarte 1998; Mariani and Alcoverro 1999; Armitage and

**Table 16.1** Herbivore seagrass preferences around the world

| Consumer | Preferences | Region | Reference |
|---|---|---|---|
| Mostly fish | *Hw* > **Tt** | South Florida, USA | Armitage and Fourqurean (2006) |
| Three fish species | *Sf* > *Hw* > **Tt** | Caribbean | Prado and Heck (2011) |
| Sea urchins | *Hw* > *Sf* > **Tt** | Caribbean | Prado and Heck (2011) |
| Dugongs | *Hu* > *Cr* > **Th** | Indonesia | De Iongh et al. (1995) |
| Fish (Scaridae) | **Tt** > *Hw* > **Tt**$^{E}$ > *Sf* | Caribbean | Lobel and Ogden (1981) |
| Fish (probable) | *Hs* = *Hu* = *Ho* > *Ca* > **Aa** = **Pa** | Shark Bay, Western Australia | Burkholder et al. (2012) |
| Dugongs | *Ho* > *Hu*$^{T}$ > *Hs* > *Si* > *Hu*$^{B}$ > **Zc** | Moreton Bay, Queensland | Preen (1992) |
| Fish (Scaridae) | *Cr* > *Si* > *Hu* = *Hw* > **Th** > **Cs** = *Hs* > **Tc** > **Ea** | Watamu marine national park, Kenya | Mariani and Alcoverro (1999) |
| Neritid gastropod | **Zc** > *Ho* > **Cs** | Moreton Bay, Queensland | Rosini et al. (2014) |
| Green turtle | **Th** > *Cr* | Lakshadweep islands, India | Kelkaret al. (2013) |

Studies include feeding preference experiments and observational studies. Observational studies (including diet studies and feeding observation studies) were only included if frequency of occurrence of food items was accounted for in the environment. In some cases herbivore preferences correlate positively to nutrient or soluble carbohydrate content of seagrass tissues, or negatively to fiber content; however, these patterns are not universal. Seagrasses with pioneer life histories are italicized; climax seagrasses are listed in bold. Non-seagrass food items are excluded. *E* epiphytes removed, *T* thin leaf morph, *B* broad leaf morph. Hw = *Halodule wrightii*, Tt = *Thalassia testudinum*, Sf = *Syringodium filiforme*, Hu = *Halodule uninervis*, Cr = *Cymodocea rotundata*, Th = *Thalassia hemprichii*, Hs = *Halophila spinulosa*, Ho = *Halophila ovalis*, Ca = *Cymodocea angustata*, Aa = *Amphibolis antarctica*, Pa = *Posidonia australis*, Si = *Syringodium isotefolium*, Zc = *Zostera muelleri* (formerly *Z. capricorni*), Cs = *Cymodocea serrulata*, Hst = *Halophila stipulacea*, Tc = *Thalassodendron ciliatum*, Ea = *Enhalus acaroides*

Fourqurean 2006; Prado and Heck 2011; Burkholder et al. 2012, Table 16.1). This pattern holds in Australian seagrass ecosystems, where fast-growing seagrasses are more readily consumed than temperate species; the latter are more likely to be targeted for their epiphytes rather than their tissue (Preen 1995; Burkholder et al. 2012). Pioneer-type seagrassess tend to be less structurally complex and higher quality food than climax seagrasses, often due to higher nutritional content, lower mechanical resistance to grazing, or both (i.e. de los Santos et al. 2012).

Seagrass physical structure can also influence top down control by generating refuge or habitat for herbivores or predators, altering habitat use patterns of fauna and, by extension, where and what they consume. For example, amphipods in beds of *Zostera marina* in San Francisco Bay, USA, associate with structurally complex inflorescences over leaves, which may be responsible for increased consumption of inflorescences and associated reduced reproductive potential (Reynolds et al. 2012). Seagrass structural complexity can also affect top down control by mediating predator-prey interactions among smaller-bodied animals. The ability of seagrasses to alter hunting efficiency and, by extension, the degree of predator control of herbivores, is predicted to have implications for mesograzer control of seagrass epiphytes (Duffy et al. 2013). For example, in mesocosm experiments where seagrass habitat complexity was manipulated (using flowering vs. simpler non-flowering shoots of *Zostera marina*), predation rates on the gammarid amphipod *Ampithoe valida* by teleost predators were reduced by half or more in the complex treatments, which was in turn associated with twice as much *Z. marina* biomass lost as in the simpler treatments (Carr and Boyer 2014). However, this relationship is not uniform; instead, the relationship between predation risk and habitat complexity is mediated by both the hunting mode of the predator and the escape mode of the prey (Wirsing et al. 2010). For example, in terrestrial old field ecosystems in New England, USA, spider predators that use a sit-and-wait hunting strategy hide in grasses, reducing grasshopper use of grasses and increasing their use of nearby herbs (Schmitz 2008). As a result, grasshopper herbivores alter the species on which they feed, changing patterns of top-down control (Schmitz 2008).

Because of the diversity of structural and chemical properties of submerged aquatic macrophytes, primary producer community assembly can mediate the effects of top down control. Seagrass that are associated with other primary producers can experience alterations in the intensity and direction of top-down control as herbivores change consumption rates or feeding preference in the context of a more diverse primary producer community. For example, the association between seagrass and seagrass epiphytes is one of the most important associations in seagrass ecosystems. Epiphytes can rapidly overgrow seagrasses, reducing light penetration and nutrient availability to seagrass tissues.. Furthermore, they can reduce seagrass fitness by attracting herbivores to seagrasses and mediating herbivore consumption of seagrass tissue. For example, when given a choice between feeding on *Posidonia australis* blades with or without epiphytes, two species of teleosts (Family *Monocanthidae*) preferentially targeted the heavily epiphytized leaves, resulting in an eightfold increase in percentage of biomass (including seagrass) removed by these herbivores (Wressnig and Booth 2007). Similar feeding preferences are apparent with the sea urchin *Lytechnius variegatus* when feeding on *Thallasia testudinum* (Marco-Mendez et al. 2012). The mediation of grazing effects on one macrophyte by another occurs on larger scales as well; in Moreton bay, Queensland, destructive excavation grazing by dugongs removes not only targeted tropical seagrasses such as *Halophila ovalis* (which quickly recovers), but also the closely associated *Zostera muelleri*, inhibiting the expansion of this climax seagrass (Preen 1995). Associations between two macrophytes may be also detrimental to a seagrass species if the preferred species is overgrazed and herbivores switch grazing to an associated seagrass to compensate, as sometimes occurs when mesograzers eliminate their algal food supply (Duffy et al. 2001, 2003).

The structural complexity created by macrophytes can also alter grazing pressure on surrounding primary producers if they create refuge for herbivores which are unwilling to venture far from the protection of cover, as occurs in the grazing halos of the Caribbean (Randall 1965). This may have positive or negative influences on associated seagrasses, depending on what the feeding preference of the grazer is, and may result in surprising interactions between macrophytes. For example, drift macroalgae in beds of the eelgrass *Zostera marina* in the York River, Virginia, USA, may indirectly reduce epiphyte loads on nearby eelgrass leaves by providing refuge for mesograzers, suggesting that the presence of competitive macroalgae at low densities may actually facilitate eelgrass persistence (Whalen et al. 2013). Seagrasses that are found in association with relatively unpalatable or chemically defended neighbors may also withstand lower rates of direct grazing by creating microsites of reduced herbivory as has been documented with algae (Hay 1986), though we are unaware of similar studies on seagrasses. The potential for this to alter herbivore pressure likely depends heavily on the spatial scales at which herbivores perceive food quality and the spatial arrangement of such an association. While undeniably complex, understanding the drivers of herbivore feeding preference is absolutely critical to predicting the net effects of consumer control in seagrass ecosystems.

### 16.2.2 The Role of Herbivores

Herbivores in seagrass ecosystems generally adhere to one of three trophic roles—epiphyte consumers, phytoplankton consumers, and macrophyte consumers. However, herbivores vary widely in their individual capacity to mediate the strength of top-down control through these pathways. Australian seagrass ecosystems feature herbivores that range in size by several orders of magnitude, from tiny arthropods and gastropods only a few millimeters across to marine mammals three meters in length.

Seagrass herbivores can be categorized into three categories based on size: mesograzers, macrograzers and megagrazers. Mesograzers are invertebrates, generally arthropods and gastropods, under 2.5 cm across (Fig. 16.1). Though mesograzer densities vary widely with locale, they can be considered cosmopolitan residents of seagrass beds. Many mesograzers facilitate seagrass persistence through the mutualistic mesograzer model, though some consume seagrass tissue (Orth and Van Montfrans 1984; Duffy and Harvilicz 2001; Reynolds et al. 2012; Rossini et al. 2014). Indeed, many invertebrates feed on or bore directly into seagrass tissues or damage them while feeding on associated epiphytes

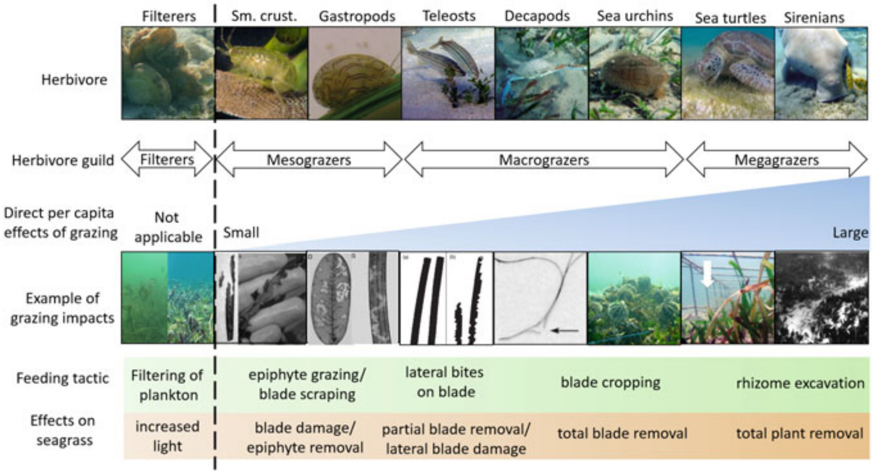

**Fig. 16.1** Examples of types of grazers found in Australian seagrass ecosystems, their feeding tactics, and the resulting impact on seagrass tissue. Tactics are listed in order of increasing per-capita effect on seagrass. Filter feeders are included for completeness, though their grazing of phytoplankton only affect seagrasses indirectly. Photos (clockwise from top left): Shark Bay Ecosystem Research Project (SBERP), Duffy et al. (2013), Rossini et al. (2014), SBERP, SBERP, SBERP, Wikimedia commons, Wikimedia commons, Preen (1995), Burkholder et al. (2013), Eklöf et al. (2008), Davis et al. (1998), Goecker et al. (2005), Rossini et al. (2014), Reynolds et al. (2012), SBERP

(e.g. Nienhuis and Groenendijk 1986; Wassenberg 1990; Zimmerman et al. 1996; Brearley and Walker 1995; Rueda and Salas 2007; Brearley et al. 2008; Holzer et al. 2011; Reynolds et al. 2012; Carr and Boyer 2014; Rossini et al. 2014). This herbivory can be widespread with significant implications for seagrass productivity and survival. For example, in the *Zostera marina* beds of San Francisco Bay, USA, consumption by the non-native amphipod *Ampithoe valida* can deplete seed stocks of this seagrass in a matter of weeks, which may reduce the genetic diversity of perennial beds or even jeopardize the persistence of annual seagrass beds which require seeds for their yearly recruitment (Reynolds et al. 2012). Similarly, the isopod *Limnoria agrostisa*, widespread throughout Western Australia, burrows into leaf sheathes of *Amphibolis griffithi* and *Posidonia* spp., consuming seagrass tissue and damaging or destroying leaf clusters (Brearley et al. 2008). The effects of seagrass consumption by *L. agrostisa* are substantial, with 40–70% of leaves being damaged and approximately 40% of leaf clusters destroyed by this species, illustrating that even small grazers can have surprisingly large effects.

Macrograzers include larger herbivores, such as sea urchins, decapod crustaceans, teleosts like parrotfish (Family *Scaridae*) and trumpeters (Genus *Pelates*), and swans (Armitage and Fourqurean 2006; Burkholder et al. 2012; Bessey et al. 2016). These herbivores may target either seagrass tissue or associated epiphytes, though in the case of the latter they still usually remove seagrass tissue in the process, making the impact of seagrass macrograzers generally negative.

For example, along the coast of the Gulf of Mexico, USA, the purple urchin *Lytechinus variegates* is able to consume the majority of aboveground seagrass biomass, sometimes leading to local seagrass extinction (Valentine and Heck 1991; Heck and Valentine 1995; Rose et al. 1999). Similar events have occurred in Australian seagrass meadows and urchin barrens in temperate algal systems are iconic. Multiple instances of overgrazing by sea urchins have contributed to losses of *Posidonia* spp.-dominated seagrass meadows on the scale of hectares in Cockburn Sound, Western Australia since 1980 (Kendrick et al. 2002). Similarly, aggregations of the urchin *Heliocidaris erythrogramma* denuded 45 ha of *Posidonia* habitat in Botany Bay, Australia, between 1979 and 1984 (Larkum and West 1990). In the Torres Straits, reduced seagrass density is correlated with high sea urchin abundance, likely as a result of intense grazing by those urchins (Long and Skewes 1996). Urchins can also overgraze *Amphibolis antarctica*, by targeting leaf meristems (Burnell et al. 2013a). Finally, Australian teleosts like the striped trumpeter *Pelates octolineatus* can be important consumers of seagrass photosynthetic tissue (Bessey and Heithaus 2015).

Though the ranges for individual species differ, mesograzers and macrograzers of some kind can be found in seagrass ecosystems around Australia. Some Australian macrograzers, like the teleosts *Pelates octolineatus*, *Odax acroptilus*, and *Haletta semifasciata*, or the urchin *Heliocidaris erythrogramma*, consume substantial proportions of seagrass and epiphytic algae as part of their diet and can, in the case of *H. erythrogramma*, strip entire areas of seagrass above-ground biomass bare (Eklöf et al. 2008; MacArthur and Hyndes 2007; Bessey et al. 2016). Both macrograzers and mesograzers, however, generally target above-ground leaf tissue and leave below ground biomass intact (Fig. 16.1).

Because of their relatively high populations in Australian coastal ecosystems, megaherbivores play a more important role in these habitats than they do in well studied seagrass ecosystems of Europe and North America (Lanyon et al 1989). Specifically, Australian seagrass ecosystems are home to two species of megaherbivores: green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*). Though both megaherbivores consume seagrass tissue, their grazing tactics generally differ. When consuming seagrass, green turtles primarily remove above ground biomass by cropping seagrass leaves, though in some areas of the world they will excavate belowground biomass as well (Christianen et al. 2014). Conversely, dugongs commonly excavate seagrass beds, particularly when Australian tropical seagrass such as *Halophila ovalis* and *Halodule uninervis* are present (Anderson 1986; Preen 1995; Masini et al. 2001). During excavation, dugongs dig into the sediment to target seagrass rhizomes, potentially destroying large areas of seagrass beds (e.g. Preen 1995, Fig. 16.1). This grazing tactic, combined with the dugong's large size, relatively high metabolic rate, and obligate seagrass diet, means dugong-seagrass interactions can be very strong. Indeed, in Shark Bay, Western Australia, dugong excavation results in the consumption of approximately 50% of primary production in beds of the pioneer seagrass *Halodule uninervis* (Masini et al. 2001). When such seagrasses are unavailable or when risk of predation makes excavation grazing unappealing, dugongs will instead crop the above ground biomass of temperate seagrasses such as those from the genera *Zostera* or *Amphibolis* (Anderson 1986; Preen 1995; Wirsing et al. 2007a). This has important implications for their impacts on seagrass community structure and ecosystem dynamics (see below).

Finally, suspension feeders play important, if underappreciated, roles in the top down control of seagrass ecosystems. Consisting of a variety of taxa including sponges, bivalves, gastropods, crustaceans, and ascidians, this herbivore group does not actually consume seagrass. Suspension feeders are, however, important herbivores in seagrass ecosystems for a similar reason to facultative mesograzers—they control primary producers (specifically phytoplankton) that compete with seagrasses for light (Peterson and Heck 2001; Newell 2004). The effect of phytoplankton removal on seagrasses is hard to quantify and disentangle from the more general benefit suspension feeders have on water clarity since suspension feeders also remove suspended sediment and particulate organic matter. However, the benefit this herbivore group has on seagrasses can be surprisingly strong due to the high light requirement of seagrasses as a group (Dennison et al. 1993). For example, mathematical models estimate that uniform densities of the Eastern Oyster *Crassostrea virginica* as low as 25 g dry weight $m^{-2}$ reduces suspended sediment concentrations by almost an order of magnitude (Newell and Koch 2004). In areas where phytoplankton loads are high, suspension feeders probably play important, if indirect, roles as seagrass facilitators.

Because the net effects of herbivores in seagrass ecosystems is heavily influenced by which grazing pathways dominate in that system, it is important to understand where specific pathways are most likely to dominate, and by extension, the geographic ranges of important herbivores. Mesograzer control of epiphytes is thought to be widespread and may overshadow the ecological effect of direct seagrass consumption in many places (see Hughes et al. 2004; Valentine and Duffy 2006). However, the dominance of the mesograzer pathway relative to other grazing pathways is likely to be limited to temperate seagrass habitats within Australia. This is due to the presence of megagrazers in tropical and subtropical Australian seagrass ecosystems, as well as the generally pioneer seagrass species that typify tropical Australian waters, the ephemeral nature of which limits the effect of epiphyte colonization. Even within temperate seagrass ecosystems, whether the net effect of herbivores is facultative or destructive towards seagrasses depends on the relative dominance of macrograzers and destructive mesograzers against facultative mesograzers and filter feeders. Indeed, most teleost and urchin macrograzers on which investigations into top down control have been done have subtropical to temperate distributions (Fig. 16.2). This range separation means that in tropical Australian systems, megagrazers should generally have a stronger potential to dominate top-down control than macrograzers or mesograzers, while in temperate habitats clear dominance of herbivore pathways are probably more elusive. All of these herbivore groups overlap in subtropical habitats, however, further complicating predictions about which pathways will dominate the effects of top down control in these habitats. For example, multiple herbivore exclosure studies in Shark Bay suggest that megagrazer and macrograzer pathways may each dominate in different habitats of the same ecosystem (Burkholder et al. 2013; Bessey et al. 2016).

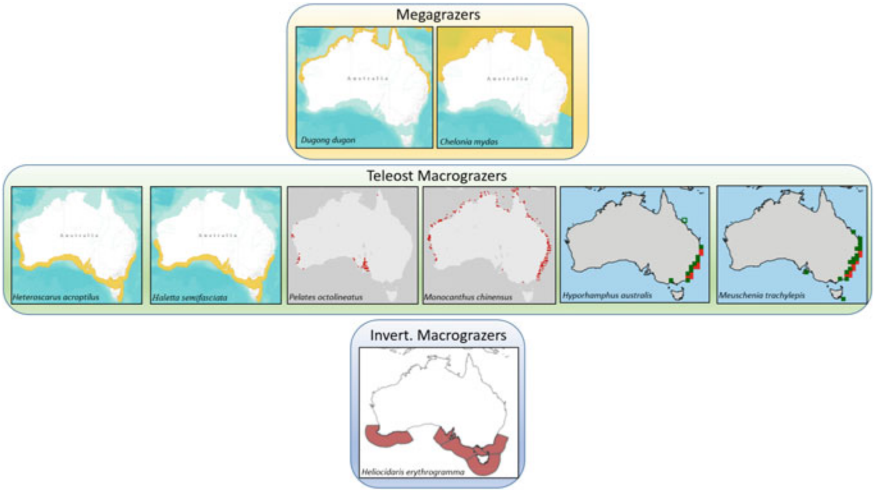

**Fig. 16.2** Known distributions of representative Australian seagrass megagrazers and macrograzers. Megagrazers are distributed tropically and subtropically while distributions of well studied macrograzer are largely temperate and subtropical; subtropical areas where ranges between megagrazers and macrograzers interact may exhibit additional complexity because of the co-occurrence of these different guilds. Ranges of macrograzers, however, may reflect geographically restricted research effort rather than true geographic range separations between macrograzers and megagrazers. Map sources by row, left to right: IUCN, IUCN, Encyclopedia of Life, Aquamaps.org, Marinespecies.org

### 16.2.3 The Role of Predators

Predators exert top-down control in seagrass ecosystems not only by regulating the populations of their prey, but also by altering the intensity, target, and spatiotemporal patterns of herbivory (Heithaus et al. 2008a, b). When this control impacts trophic levels below that of their prey, a trophic cascade occurs (Paine 1980). The potential role of predators in shaping patterns of top-down control by seagrass herbivores has been recognized for decades. As has been mentioned before, for example, Randall (1965) suggested that grazing halos around Caribbean patch reefs were due to reef-associated fishes that targeted seagrass but were unwilling to venture far from the safety of their refuges. Since then, meta-analysis has indicated that trophic cascades tend to be strongest in benthic marine ecosystems (Shurin et al. 2002; Borer et al. 2005).

Traditionally, trophic cascades were thought to operate exclusively through lethal predator effects in which increases in predator abundance reduce mesoconsumer density through predation and, as a result, also reduce pressure on associated resource species (Lima 1998). Predators, however, elicit myriad changes in prey behavior including fear-induced habitat shifts, reduction in foraging rates, or changes in diet (e.g. Randall 1965; Lima 1998; Brown et al. 1999; Peacor and

Werner 2001; Heithaus and Dill 2002, 2006; Brown and Kotler 2004) and traits including morphology and physiology (e.g. Creel et al. 2007). These “risk effects” of predators can initiate or enhance trophic cascades through trait-mediated indirect interactions (i.e. TMIIs, Werner and Peacor 2003; Dill et al. 2003; Schmitz et al. 2004; Preisser et al. 2005).

One type of TMII, a behaviorally mediated indirect species interaction (BMII; sometimes referred to as a behavior-mediated trophic cascade; BMTC), occurs when changes in a property of one species (the “initiator”) cause a behavioral shift in a “transmitter” species, which in turn induces a change in a property of a third species (the “receiver”) (Schmitz et al. 1997; Dill et al. 2003). BMII have received considerable attention recently in terrestrial, freshwater, and intertidal marine systems and appear to be capable of affecting populations and communities at magnitudes equal to, or greater than, those of lethal effects of predators (e.g. Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005). The power of such non-consumptive predator effects stems from their ability to affect many prey simultaneously, and sometimes through the ability of prey to exhibit compensatory population growth in response to mortality from consumption by predators. Additionally, in some situations BMII can reverse the sign of indirect interactions between top predators and basal resources in food chains with an odd number of trophic levels relative to those predicted by lethal effects of predators alone (Dill et al. 2003; Heithaus and Dill 2006; Wirsing et al 2007c). Importantly, even if predators rarely consume or have minimal effects on the equilibrium population sizes of mesoconsumers, they may still trigger trophic cascades through non-lethal mechanisms by altering where and at what rate mesoconsumers exploit resource species (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; Heithaus et al. 2008a, b). Finally, the effects of direct predation and risk effects interact with one another to enhance overall predator effects and this interaction may account for the majority of predator impacts (Werner and Peacor 2003; Heithaus et al. 2012).

Most trophic cascades recorded in Australian marine ecosystems have been from temperate and tropical algae reefs (Pinnegar et al. 2000), not seagrass ecosystems. However, this may be due not to a lack of trophic cascades in seagrass ecosystems so much as to a gap in research effort. Indeed, long term studies in Shark Bay, Western Australia, have identified multiple trophic cascades (and BMIIs) in a subtropical seagrass ecosystem. Shark Bay’s apex predator, the tiger shark (*Galeocerdo cuvier*) induces habitat shifts at multiple spatial scales in both herbivores and mesopredators. Specifically, dolphins (*Tursiops aduncus*), dugongs, and cormorants (*Phalacrocorax varius*) all shift from foraging primarily in productive shallow seagrass habitats when sharks are scarce to foraging mainly in less productive, but safer, deep habitats when shark densities are high (Heithaus and Dill 2002; Heithaus 2005; Wirsing et al. 2007b). Dolphins and dugongs that continue to forage over shallow habitats when sharks are present largely abandon the highly dangerous interior portions of shallow banks that they used when sharks were scarce, in order to have easy escape options near bank edges (Heithaus and Dill 2006; Wirsing et al. 2007c). Similarly, green turtles in good body condition forage almost exclusively along bank edges, where seagrass quality is lower, when sharks are present but move toward interior microhabitats, with higher seagrass quality, when tiger sharks are scarce (Heithaus et al. 2007). Furthermore, tiger sharks alter dugong foraging tactics, limiting destructive excavation grazing that has been recorded to destroy hectares of seagrass elsewhere (Wirsing et al. 2007a; Preen 1995). None of these spatiotemporal shifts can be explained by variation in food availability, water temperature, or other factors. In the case of megaherbivores, these predator effects cascade down to the seagrass bed, altering which seagrasses dominate on bank edges (Burkholder et al. 2013, Fig. 3).

These studies exemplify the potentially dramatic effects predators can have in seagrass ecosystems through regulating the behavior of their prey, yet the dominant predators and herbivores in Australian seagrass ecosystems differ across the continent. While large-bodied sharks are undoubtedly the largest apex predators commonly found in most seagrass ecosystems, dolphins are also important and widespread upper trophic level predators. Several species of dolphins are found in coastal seagrass ecosystems of Australia–Indo-Pacific bottlenose dolphins (*Tursiops* sp.) and humpback dolphins (*Sousa sahulensis*) being common. Both species are piscivores, and because of high mammalian metabolic rates likely consume a large number of teleosts that may be important in the dynamics of seagrass ecosystems. In the subtropical Shark Bay seagrass ecosystem, *Tursiops* cf. *aduncus* preys upon striped trumpeters (*Pelates octolineatus*) (Heithaus and Dill 2002), the dominant teleost grazers (Heithaus 2004; Burkholder et al. 2012). Given the high population densities of dolphins in Shark Bay (Preen et al. 1997; Heithaus and Dill 2002) it is possible that dolphins could indirectly influence seagrass ecosystems through modifying the population sizes or spatiotemporal patterns of foraging by *P. octolineatus.* Unfortunately, little work has focused on the potential for dolphins to impact the dynamics of fish populations within seagrass ecosystems or how those impacts may cascade to structure seagrass communities.. Similarly, pinnipeds such as Australian sea lions (*Neophoca cinerea*) and fur seals (*Arctocephalus* spp.), may have been important predators in temperate Australian seagrass ecosystems, but their population sizes are much reduced from historical levels and the potential role of pinnipeds in structuring Australian seagrass ecosystems has not been explored. While both pinniped species tend to forage in offshore habitats, using coastal habitats for transit and rest, some individual Australian sea lions do forage consistently in coastal seagrass habitats (Lowther et al. 2011) and could exert top-down impacts on fishes of seagrass beds. This possibility remains largely unexplored, and studies of the potential top-down roles of predatory marine mammals in Australian seagrass ecosystems remains an interesting and potentially significant avenue of inquiry.

Unsurprisingly, many teleosts and smaller elasmobranchs may play important roles in Australian seagrass ecosystems. Indeed, small sharks (<2 m total length), rays, and teleosts can be locally abundant in Australian seagrass communities (e.g. White and Potter 2004; Simpfendorfer and Milward 1993). While some of these predators are actually omnivorous, consuming primary producers in addition to animal matter (e.x. *P. octolineatus*, Belicka et al. 2012; Burkholder et al. 2012;

Bessey and Heithaus 2015), other mesoconsumers feed on a diversity of prey including infauna, cephalopods, crustaceans, and worms, which may initiate trophic cascades. For example, stingrays may initiate three-step trophic cascades under which consumption of filter-feeding bivalves results in increased phytoplankton load, reducing light penetration to seagrass tissues. Indeed, there is strong evidence for the capability of batoids to exert top down control over bivalves when these predators are locally abundant (e.g. Myers et al. 2007), though to our knowledge empirical work on the indirect effects of batoids on seagrass are lacking. Similarly, marine birds have the potential to exert top-down control through direct predation and risk effects (i.e. Bessey and Heithaus 2013). Like predatory marine mammals, marine birds such as cormorants have high metabolic rates and can exist at high densities in seagrass ecosystems (e.g. in Shark Bay, Heithaus 2005; Bessey et al. 2016). Furthermore, the proportion of teleosts in the diets of cormorants in Australia can reach 90% or more (del Hoyo et al. 1992; Blaber and Wassenberg 1989; Humphries et al. 1992), and daily consumption rates can be 15% of body mass or more (Humphries et al. 1992). Interestingly, the role of these mesopredators in generating top-down control (specifically trophic cascades) remains largely unexplored in Australian seagrass ecosystems.

Trophic cascades have been recorded or proposed in seagrass ecosystems at multiple scales and trophic levels worldwide, from control of seagrass associated invertebrates by predatory teleosts (Heck and Valentine 1995; Heck et al. 2000; Lewis and Anderson 2012; Carr and Boyer 2014) to behavioral control of mega-herbivores and secondary predators by tiger sharks (Heithaus et al. 2012; Burkholder et al. 2013). As with herbivores, however, predators do not have equal capacity to exert top-down control or trophic cascades in seagrass ecosystems. Because herbivores influence seagrass communities through two main avenues (direct consumption of seagrass biomass and consumption of seagrass competitors), predators ultimately exert top-down control through these two pathways. In areas where megagrazers are dominant, large sharks are the only apex predators likely to have significant capability to structure seagrass ecosystems through top-down control. Conversely, if smaller teleost herbivores mediate a direct seagrass consumption pathway, intermediate predators such as dolphins, pinnipeds, cormorants and small sharks may all influence the potential for a cascade to occur. Finally, because so many members of the epiphyte-consuming mesograzers are small-bodied invertebrates, myriad intermediate predators may exert top-down control. Though studies evaluating predator control of megagrazers are exceedingly rare, the prominence of megaherbivores in tropical and subtropical Australian seagrass ecosystems means that large-bodied sharks may be, or may have been, disproportionately important to structuring these ecosystems. For example, the loss of large sharks is hypothesized to be important in allowing the release of sea turtles in several seagrass ecosystems that has resulted in considerable declines in seagrass biomass (e.g. Heithaus et al. 2014) and potential ecosystem collapse (Christianen et al. 2014). Conversely, endothermic intermediate predators like dolphins and pinnipeds may be more important to structuring temperate seagrass ecosystems.

### 16.2.4 The Role of Food Web Structure

To understand the role of top down control, particularly trophic cascades, it is helpful to be able to predict when and where such cascades are most likely to occur. Ecological theory predicts that food web structure, specifically food web length and complexity, will have important effects on the strength and nature of such top down control. In very simple food webs, the number of links between apex predators and primary producers has implications for whether herbivore control on primary producers is strong or weak. Chains with an odd number of linkages should yield weak herbivore control on primary producers and a facultative relationship between apex predators and primary producers through a trophic cascade. Conversely, chains with an even number of levels should yield strong herbivore control of primary producers and an inhibitive effect of apex predators on primary producers as those larger predators regulate intermediate predators, which in turn control herbivores. Assuming that populations are density dependent and limited by food or predation, simple food webs are most sensitive to food chain length because trophic cascades remain strong, having little opportunity to attenuate and diffuse through multiple food web pathways (Strong 1992). Accordingly, ecosystems with simple trophic structure are more likely to suffer from reversals in the "direction" of trophic cascade effects and concomitant changes in the strength of herbivore control on plants if the initiator species (a predator) is removed.

While food chain length influences the net direction of the effect apex predators and herbivores will have on primary producers, food web complexity can often influence how strong those effects can be. This is because the strength of trophic cascades is dependent on the strength of species-species interactions—and the simple construction of food chains leads them to be more likely to have strong species interactions than complex food webs. In simple linear food webs (i.e. food chains), the interaction strengths between predators, herbivores, and resource species is necessarily strong, because consumptive relationships are "unified" (*sensu* Strong 1992) into single species-species interactions (Fig. 16.4). Complex food webs, however, have multiple trophic or interaction pathways from apex predators to primary producers, and these pathways may not have the same number of links. This can diffuse predator effects through many avenues, resulting in fewer of the strong species-species interactions that are typical of linear food webs and attenuating the overall indirect effects of a predator on primary producers (Fig. 16.4). While species diversity increases food web complexity, generalists and omnivores also do so by consuming organisms from multiple trophic levels, creating additional pathways through which predator control can operate. For example, if herbivores are generalists, their negative effects on primary producers may be attenuated through their indiscriminate consumption of resource species, reducing the strength of competitive interactions among seagrasses or between seagrass and epiphytic or benthic algae.

Though increased food web complexity likely reduces the probability of strong species-species interactions (and by extension, strong trophic cascades), they can still occur. But what makes a strong interaction between species? In general, strong interactors are species that are "efficient" (Strong 1992); they may consume more prey per capita, or have strong non-consumptive effects. Most seagrass food webs display some trophic complexity and tend to have multiple trophic channels from apex predators to primary producers—but they can also be dominated by channels with strong interactions that remain undiffused, increasing the likelihood of trophic cascades. This is exemplified in tropical seagrass ecosystems dominated by megagrazers like adult and large juvenile green turtles and dugongs that are almost exclusively at risk from tiger sharks (e.g. Heithaus et al. 2008b; Heithaus 2013; Wirsing et al. 2007a, b, c). The loss of this top predator could not be compensated for by increased predation rates or predation risk from another predator. Megagrazers, in turn, tend to have strong per-capita effects on seagrasses and are thus strong interactors with these primary producers (i.e. Figs. 16.3, 16.4). When this short, three-link chain is the dominant trophic pathway, seagrass ecosystems

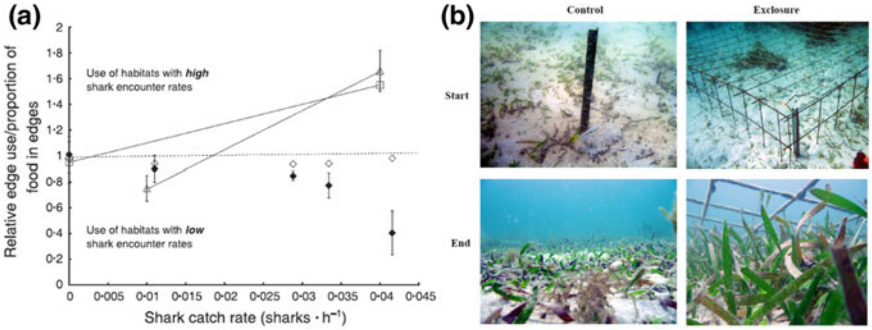

**Fig. 16.3** **a** Change in habitat use of dugongs (open triangles), indo-pacific bottlenose dolphins (open squares), and pied cormorants (closed diamonds) associated with changes in abundance of large sharks in Shark Bay, Western Australia. Open diamonds represent the food supply of cormorants. The dashed line represents expected proportion of habitat use if fauna are ideally distributed in relation to their food supply; values above the line represent over-use of seagrass edge habitats, where the chance of tiger shark encounters is highest. Dugongs and dolphins move into edges of seagrass banks when sharks are abundant, choosing to increase predator encounter frequency in exchange for a higher probability of escape to deep water. Cormorants, the escape success of which is independent of benthic terrain, seek to minimize predator encounters and increase use of seagrass meadow interiors when sharks are abundant. This interesting finding illustrates the complex and sometimes counterintuitive nature of predator prey interactions in seagrass ecosystems, and the need to consider properties of predators, prey, and landscape in predicting the effects of antipredator behavior. **b** Megagrazer exclosure experiments in seagrass edges confirm that habitat use patterns of megaherbivores translate to increased top-down control of seagrass edge habitats, signifying a behaviorally mediated trophic cascade from tiger sharks to the seagrass community. Reproduced from Heithaus et al. (2009) and Burkholder et al. (2013)

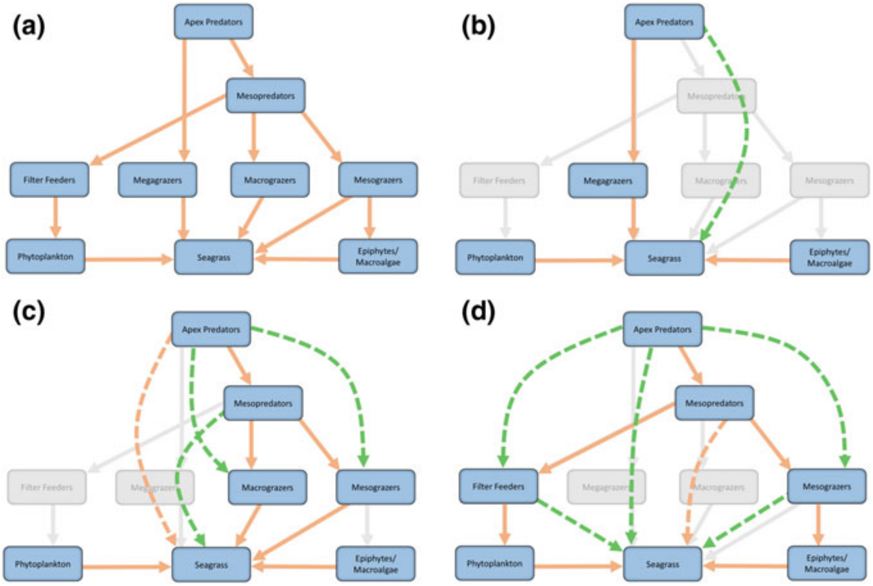

**Fig. 16.4** Conceptual food webs illustrating the main direct and indirect pathways through which top-down control operates in seagrass ecosystems. Arrow direction indicates the primary flow of the interaction, while colors indicate positive (green) or negative (orange) effects of one group on another. Solid lines indicate direct effects; dashed lines indicate indirect effects (primarily trophic cascades). Greyed out boxes and lines indicate minor consumers and pathways, depending on the example. An intact seagrass community (**a**) showing direct effects only; the potential for trophic cascades and strong indirect effects depends on which pathways dominate through the strongest interactors. When the megagrazer pathway is dominant (**b**), apex predators can generate trophic cascades that benefit seagrasses by reducing grazing by megagrazers. This pathway has been lost from many tropical and subtropical seagrass ecosystems due to overharvest of these grazers, though it's likely to still dominate throughout much of tropical and subtropical Australia. When smaller seagrass herbivores are the dominant interactors (**c**), mesopredators may initiate a three step trophic cascade that reduces grazing, while mesopredator control by apex predators may initiate a four step cascade that releases grazers and strengthens consumer control of seagrasses. In some ecosystems, mutualistic relationships dominate (**d**), led not only by mesograzers that consume competitive epiphytes and macroalgae, but also by suspension feeders which remove phytoplankton, increasing light penetration to seagrass tissues. Note that indirect interactions tend to be positive when traveling down an odd number of steps, but negative at even numbers of steps

are prone to strong trophic cascades—and by extension, highly vulnerable to predator removal. Consequently, the loss of apex predators like large sharks in these ecosystems may have disproportionate effects on the primary producers of Australian seagrass ecosystems (e.g. Burkholder et al. 2013; Heithaus et al. 2014) (Fig. 16.5).

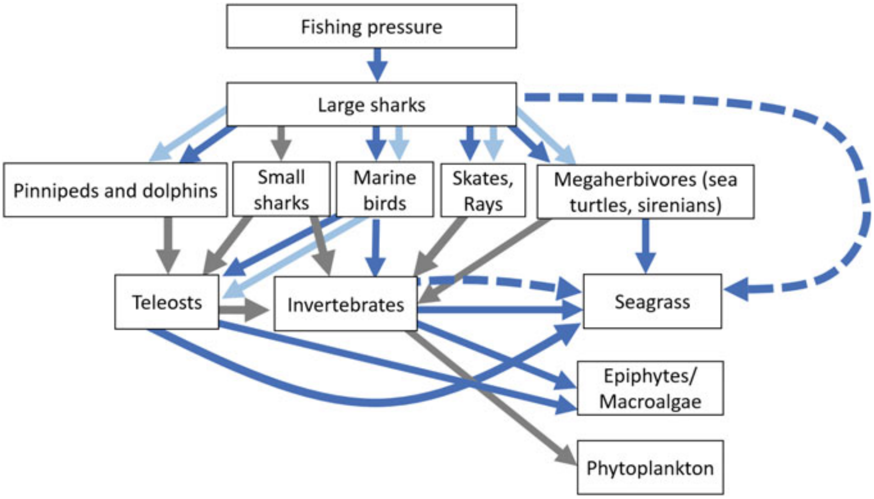

**Fig. 16.5** Interaction web highlighting potential connections between large shark removal and lower trophic levels. Individual linkages are denoted by colored arrows; dark arrows indicate consumptive effects while light arrows indicate behavioral effects; dotted lines indicate indirect effects. Only relationships between groups that have been attempted to be quantified have been shown. Interactions which have been observed in Australian seagrass ecosystems are shaded blue. Note a lack of studies on interactions of Australian seagrass-associated teleosts and invertebrates, as well as a general lack of empirical, quantitative estimates of indirect effects, which may be common given the large number of species interactions that typify apex predators. Modified from Ferretti et al. (2010)

## 16.3 Effects of Consumers on Seagrass Communities

Consumers can structure seagrass communities through consumption or facilitation of primary producers, alteration of community composition, or through influencing bottom-up processes. These forms of top-down control, by altering the properties of seagrass habitats, can drive seagrass ecosystem processes, functions and services at local, regional, and global scales.

### *16.3.1 Ability of Consumers to Facilitate Seagrasses*

Seagrasses provide substrate for epiphytes, which compete with them for resources such as light. High nutrients often increase epiphyte and phytoplankton loads with negative impacts for seagrasses; indeed, eutrophication is one of humanity's most pervasive stressors to seagrass ecosystems (Waycott et al. 2009). By consuming epiphytes and plankton, mesograzers and suspension feeders have the capacity to attenuate the negative effects of eutrophication in seagrass ecosystems (Peterson and Heck 2001; Valentine and Duffy 2006). The role of facultative mesograzers has been particularly well supported with empirical data—historically in the laboratory and mesocosms, but increasingly in the field. Early caging work in Western Australian *Posidonia sinuosa* beds showed that gastropods reduce epiphyte biomass by almost 50%, while amphipods have minimal effects on epiphyte biomass (Jernakoff and Nielsen 1997). Novel cage-free approaches, using slow-release pesticides, have made manipulating invertebrate densities in benthic marine ecosystems easier without introducing caging artifacts (Poore et al. 2009). These experiments, several of which have been conducted in Australian seagrass ecosystems, confirm the importance of invertebrate mesograzers to epiphyte control. For example, exclusion of amphipod mesograzers from seagrass meadows in Cockburn sound,, Western Australia, resulted in significant increases in epiphyte biomass in some seagrass species, though this did not translate to increases in seagrass biomass over the experiment duration (7 weeks) (Cook et al. 2011). Similar cage-less experiments in the *Posidonia angustifolia* beds of Lady Bay, South Australia that manipulated mesograzer densities and nutrient levels showed that such grazers are able to compensate for increased nutrient additions by increasing their per-capita consumption of seagrass epiphytes (McSkimming et al. 2015), mirroring findings elsewhere (i.e. Chesapeake Bay, USA, Reynolds et al. 2014). Indeed, in general, mesograzer presence reduces epiphyte loads approximately as much as nutrient enrichment in the water column increases them: effect sizes are often similar in magnitude but opposite in effect (Hughes et al. 2004; Heck and Valentine 2006).

Mesograzers, and to a lesser degree filter feeders, have received the most attention for their ability to mitigate nutrient enrichment effects, but other consumers are able to do so as well. Larger herbivores, even if they do not target epiphytes, can also be strong controllers of epiphyte biomass in the face of eutrophication (Heck et al. 2000; Goecker et al. 2005; Brodeur et al. 2015; Reynolds et al. 2014). For example, clipping experiments mimicking green turtle grazing in beds of *Halodule uninervis* off of the Derawan Island, Indonesia, almost doubled seagrass production in the face of increased nutrient loads, and may be an important mechanism for exporting excess nutrients from the system, thereby limiting epiphyte overgrowth (Christianen et al. 2012). This top-down facilitation may act as a critical source of resilience for seagrass communities—particularly those near urban centers. Some have even suggested that eutrophication impacts are so large in modern seagrass ecosystems because consumer populations have been largely compromised (Burkepile and Hay 2006; Heck and Valentine 2007). Indeed, factorial experiments in Chesapeake Bay, USA indicated that nutrient additions had minor effects on seagrass productivity when in the presence of grazers, but that grazer exclusion resulted in a sixfold increase in epiphyte biomass and a 65% decrease in seagrass biomass (Reynolds et al. 2014). Perhaps most importantly, these two factors interacted significantly; in the presence of grazers, nutrient additions increased seagrass biomass, while in the absence of grazers, additions reduced biomass (Reynolds et al. 2014). As a result, maintenance of grazer populations has been suggested as a possible tool to combat the negative effects of eutrophication (e.g. Hughes et al. 2004; Reynolds et al. 2014). This suggests that successful seagrass restoration in eutrophic ecosystems will require a combined effort to reduce nutrient loads and maintain healthy populations of epiphyte herbivores (Reynolds et al. 2014). Such facilitation, however, probably has limits (Ghedini et al. 2015); for example, in rocky shore communities of the northwest Atlantic Ocean and Baltic Sea, increased nutrient loads reduce the ability of herbivores to control filamentous algae (Worm and Lotze 2006). Further work is needed to determine when mesograzers are able to control eutrophication derived epiphyte overgrowth, and under what conditions such control results in measureable benefits to seagrass (Cook et al. 2011), as the effects of epiphyte reduction may attenuate at the seagrass-epiphyte interface, and because mesograzers can also have substantial negative effects on seagrass production (e.g. Lewis and Anderson 2012). Lastly, grazers may also facilitate particular seagrass species by removing non-epiphyte competitors such as macroalgae or other seagrasses (see Sect. 3.3, below).

In addition to stimulating seagrass production by inducing compensatory responses to low levels of direct herbivory and through removing competitive epiphytes, consumers can exert top down control by facilitating seagrass reproduction or seed dispersal. Though many organisms are destructive seed predators of seagrass ecosystems, highly mobile seed consumers can also facilitate dispersal and sexual reproduction (Sumoski and Orth 2012). Herbivores may even act as pollinators, as is thought to occur with crustacean and polychaete mesograzers in *Thalassia testudinum* beds (van Tussenbroek et al. 2012). Finally, through active seed dispersal, consumers have the ability to increase genetic connectivity between seagrass communities or promote colonization up currents—something that can be difficult to achieve with passive dispersal alone.

### *16.3.2 Ability of Consumers to Damage Seagrasses*

While top down control can facilitate seagrasses, work over the past few decade has highlighted the detrimental potential of direct seagrass herbivory. Seagrasses generally display a nonlinear response to grazing; low and moderate grazing can stimulate growth and production up to a threshold, while some seagrasses simply resist or tolerate low grazing intensity; however, intense grazing can cross this threshold and jeopardize seagrass persistence (Valentine et al. 1997; Cebrián et al. 1998; Vergés et al. 2008). Concentrated grazing pressure which inhibits seagrass ecosystem function is known as overgrazing (sensu Eklöf et al. 2008). Overgrazing is most common when herbivore densities peak or where herbivore feeding tactics are particularly destructive. These events, though generally rare and usually temporally restricted, can generate strong and lasting detrimental effects on seagrass ecosystems—in extreme cases, even resulting in a complete ecosystem change (see examples in Eklöf et al. 2008). All three main herbivore groups that consume seagrasses (mesograzers, macrograzers, and megagrazers) are capable of overgrazing them (e.g. Nakaoka 2002, 2005; Holzer et al. 2011; Lewis and Anderson 2012; Preen 1995; Eklöf et al. 2008).

In addition to consuming seagrass photosynthetic tissue, herbivores can also impact seagrass communities by reducing seagrass reproductive success. Mesograzers and macrograzers feed on seagrass reproductive tissues such as inflorescences, seeds, and fruits, either directly off of the plant or from the sediment surface (e.g. Wassenberg 1990; Holbrook et al. 2000; Orth et al. 2006b; Vergés et al. 2006; Reynolds et al. 2012). Some species like *Thallasia testudinum* and *Halodule wrightii* appear to be pollen limited—so herbivores may be important in limiting reproduction in these species if consumption rates of male flowers are high (van Tussenbroek and Muhlia-Montero 2012). In some cases, consumptions of flowers, fruits and seeds can result in large reductions in seed populations and thus reproduction via seeds. For example, tanaied crustaceans consume 14–27% of the seeds of *Zostera marina* and *Z. caulescens* in Japanese seagrass beds (Nakaoka 2002), while crustacean seed predators in southern California, USA, consume infloresences and up to half of *Phyllospadix torreyi* seeds (Holbrook et al. 2000). Similarly, in seagrass beds off of Rottnest Island, Western Australia, crustacean seed predators can remove more than half of tethered *Posidonia australis* seeds in a single day (Orth et al. 2006b).

Finally, negative top-down control of seagrasses can occur through non-consumptive means. By using seagrass as shelter, some animals cause damage to seagrass shoots with surprising frequency (e.g. van Tussenbroek and Brearley 1998; Brearley et al. 2008). For example, in a Mexcian Carribbean lagoon, the isopod *Limnoria simulate* burrows into the leaf sheathes of *Thallasia testudinum*, where it reproduces; average infestation rates can approach 50% and cut leaf growth by 30% when infestation rates on an individual ramet are high (van Tussenbroek and Brearley 1998). Instead of burrowing into seagrasses, other invertebrate consumers use seagrass as substrate, inhibiting light penetration to seagrass tissues and reducing growth (e.g. Long and Grosholz 2015). Through excavation of sediment and disturbance of seagrass rhizomes, stingrays can damage, destroy, or inhibit the expansion of seagrass beds while foraging for bivalves (e.g. Orth 1975). These examples illustrate the diversity of non-consumptive avenues through which top down control can inhibit the growth, expansion or persistence of seagrass ecosystems. However, further work is needed to evaluate the capability for such forces to structure seagrass communities relative to consumptive effects, which are better studied.

### 16.3.3 Alteration of Seagrass Community Composition

In general, the impacts of top down control on seagrasses are not uniform in communities with multiple seagrass species and may result in shifts in community composition and standing biomass. Such impacts are most pronounced in diverse seagrass communities of the subtropics. As previously mentioned, herds of dugongs in subtropical Moreton Bay, Queensland, focus their feeding on mixed species seagrass beds, primarily excavating the nutrient rich tropical seagrass *Halophila ovalis* but incidentally removing the climax species *Zostera muelleri*. Dugongs facilitate *H. ovalis* beds, which are able to recover quickly from grazing. Conversely, grazing prevents the expansion of *Z. muelleri*, which is disturbance-intolerant. Indeed, dugong exclusion over six months resulted in a five-fold increase in the shoot density *Z. muelleri* and a six-fold decrease in the pioneer species *H. ovalis*, while simulated dugong grazing increased shoot densities of *H. ovalis* at a rate five times faster than for *Z. muelleri.* Such feeding behavior can keep seagrass ecosystems in early successional, pioneer states dominated by fast growing, disturbance tolerant species (Preen 1995; Aragones and Marsh 2000).

Green turtles can also shift the species composition of seagrass communities.. In India's Lakshadweep Archipelago, grazing by high densities of green turtles exceeded production of the dominant seagrass species *Thalassia hemprichii* and *Cymodocea rotundata*, and resulted in reduced shoot elongation rates and a community shift from the preferred climax seagrass *Thalassia hemprichii* to a pioneer species *Cymodocea rotundata* (Kelkar et al. 2013). Similarly, a 600-day megagrazer exclusion experiment in seagrass habitats in Shark Bay, Western Australia, resulted in an eightfold decrease in shoot density of the pioneer seagrass *Halodule uninervis* and a concurrent doubling in shoot density of the larger seagrass *Cymodocea angustata* (Burkholder et al. 2013). These cages excluded megagrazers only, reaffirming the strong effects these consumers can have on seagrass community composition and reinforcing their probable general importance to top down control of Australian tropical and subtropical seagrass ecosystems. Teleost grazers can also drive shifts in seagrass community composition; reef fish in south Florida (USA) preferentially consume the pioneer species *Halodule wrightii*, facilitating the dominance of the climax seagrass *Thalassia testudinum* (Armitage and Fourqurean 2006). In each of these cases, knowledge of seagrass life history traits, consumer feeding preferences, and grazing tactics are critical to determining which seagrass species dominate. Since pioneer seagrasses cannot generally match the ecosystem functions of climax species, these shifts in community composition can translate to important changes in the functions of seagrass beds.

### 16.3.4 Effects of Consumers on Ecosystem Function

As ecosystem engineers, seagrasses serve myriad ecological functions. Seagrasses influence processes such as nutrient cycling, sediment stabilization, and carbon storage (Orth et al. 2006a, b; Fourqurean et al. 2012; McLeod et al. 2011). Seagrasses also act as important habitat and nurseries for fauna (Heck et al. 2003). Many of these functions are much more pronounced in climax seagrasses than smaller, ephemeral species. The effects of top-down control on ecosystem function is dependent on the type and intensity of seagrass herbivory that occurs. For example, moderate levels of grazing by sea urchins grazing can stimulate nutrient recycling, while higher levels of grazing can remove seagrass beds almost entirely (e.g. Eklöf et al. 2008). In seagrass ecosystems in the Gulf of Mexico, sea urchins (*Lytechinus variegatus*) alter the above-ground biomass, shoot architecture, and seagrass density so much through their grazing that they appear to reduce the refuge capabilities of the seagrass beds and facilitate their own predators (Heck and Valentine 1995). Similarly, overgrazing by unusually high densities of *L. variegatus* in Florida Bay, USA resulted in losses of >80% of seagrass biomass over more than 80 ha, altering sediment structure and promoting resuspension of fine sediments (Rose et al. 1999). Such functional alterations can increase light attenuation, reduce the resilience of seagrass beds and promote shifts to alternate, seagrass depauperate states (Orth et al. 2006a, b; Van der Heide et al. 2007, 2011). The associated loss of function from overgrazing can not only affect seagrass habitats, but also nearby habitats which depend on the ecosystem services seagrass ecosystems provide. In fact, loss of seagrass ecosystem function has implications on local to global scales. For example, seagrass loss can affect local faunal communities within and beneath seagrass beds (Heck et al. 2003; Rose et al. 1999; Thompson et al. 2014; Nowicki unpublished data), but also alters the amount of carbon sequestered in seagrass tissues and stored in sediments, influencing the role of seagrass ecosystems in the global carbon cycle (Fourqurean et al. 2012). Even apex predators can influence seagrass ecosystem function, through the trophic cascades they generate. Indeed, seagrass loss through overgrazing and extreme bioturbation have been linked (at least partially) to predator removal in these ecosystems, with implications for carbon sequestration and other functions (Heithaus et al. 2014; Atwood et al. 2015).

### *16.3.5 Effects of Consumers on Bottom up Processes*

The previous example shows how top-down control can alter seagrass ecosystem function indirectly by altering bottom-up processes like sediment stabilization. However, consumers can also alter bottom-up processes directly—a form of top-down control rarely emphasized. Seagrass-associated fauna can do this by acting as nutrient subsidies, altering environmental variables, or changing chemical properties of seagrass ecosystems. For example, avian predators that hunt far from seagrass beds but rest above or adjacent to them can generate nutrient subsidies by transporting nutrient rich guano and concentrating into these habitats, stimulating seagrass productivity and changing seagrass community composition (Powell et al. 1991; Fourqurean et al. 1995). Similarly, the defecation and excretion of fish that seek shelter on coral reefs also provide a nutrient subsidy to nearby seagrass meadows (Dewsbury and Fourqurean 2010; Allgeier et al 2013). On a larger scale, sea lions (*Neophoca cinerea*) and fur seals (*Arctocephalus* spp.) native to temperate Australian waters deposit nutrients near their haul out sites through excretion. In Seal Bay Conservation Park, Kangaroo Island, South Australia, such defecation by the resident population of ~1100 sea lions contributes approximately 3800 kg of nitrogen to the surrounding ecosystem annually (Lavery et al. 2015). This represents a considerable allochthonous source of nutrients which links pelagic productivity to coastal ecosystems, and is likely to be important to the structuring of seagrass ecosystems near pinniped colonies. Sharks may also play a role as nutrient transporters not only by coupling seagrass ecosystems with offshore pelagic ecosystems, but also by linking distant coastal ecosystems. For example, tiger sharks (*Galeocerdo cuvier*) in Australia regularly move hundreds to thousands of kilometers, spending time in both coastal and pelagic zones (Heithaus et al. 2007; Holmes et al. 2014; Ferreira et al. 2015). It should be noted that consumers can, of course, also transport nutrients out of seagrass ecosystems and that the effects of top-down alterations to nutrient cycling ultimately depends on the underlying nutrient characteristics of the surrounding environment. For example, large nutrient subsidies from a local seal colony are likely to exacerbate the effects of nutrient pollution from nearby anthropogenic sources, while consumer driven nutrient export in oligotrophic seagrass ecosystems may intensify nutrient limitation in these habitats, and vice versa.

Consumers can increase nutrient availability to seagrass ecosystems even if they themselves are immobile. For example, sponges can also alter bottom-up processes by processing nutrients in the water column, increasing their bio-availability to seagrasses (Archer et al. 2015). Similarly, bivalves concentrate nutrients in seagrass beds by consuming pelagic plankton and excreting their waste under the canopy (Peterson and Heck 2001). In addition to concentrating nutrients in seagrass beds, bivalves alter bottom-up processes in seagrass beds by altering the chemical and physical environment. Sulfur-oxidizing bivalve-bacteria symbionts are associated with most seagrass species and have been shown to increase seagrass biomass production in the face of sulfide additions (van der Heide et al. 2012). This mutualism is important, because marine sediments are generally anoxic and seagrasses expend large amounts of energy to pump oxygen gained from photosynthesis into below-ground tissues to create an “oxic microshield,” which protect below-ground tissues from chemically reduced toxins (Borum et al. 2007). This need for protective oxygen drives the high light requirements of seagrasses and makes them highly sensitive to disturbance—particularly to reductions in water quality (Borum et al. 2012). Interestingly, a trophic cascade influencing this process have been recorded whereby preferential consumption of the filter feeding bivalve *Dosinia isocardia* by the Red Knot (*Calidris canutus*) reduces competition for particulate organic matter (POM) with a second bivalve *Loripes lucinalis. L. lucinalis* derives energy from both filter feeding and through chemosynthetic bacterial symbionts. Predation on *D. isocardia* may reduce competition for POM and allow *L. lucinalis* to de-emphasize chemosynthetic pathways of energy production, which may result in higher concentrations of toxic porewater sulfide (Van Gils et al. 2012). As can be seen, top-down control through the manipulation of bottom-up processes can be important in structuring the chemical, nutrient, and physical environment in which seagrasses live, with implications for the persistence of seagrass ecosystems.

## 16.4 Top Down Control and Human Impacts

Humans are altering ecosystems worldwide, and seagrass ecosystems are no exception. All told, there are five major threats to marine biodiversity, all of which occur in seagrass ecosystems: overexploitation, physical habitat modification, sediment and nutrient pollution, invasive species, and climate change (Norse 1993; Waycott et al. 2009). Herbivores can either attenuate or amplify the effects of anthropogenic disturbance, and indirect effects that predators generate can further complicate these relationships. Yet it remains critical to understand how top down control both affects and is affected by human alterations to seagrass ecosystems. We focus here on four of the most pervasive threats to seagrass ecosystems and how they are likely to interact with patterns of top-down control: nutrient pollution, overfishing of marine consumers, invasive species, and climate change.

### *16.4.1 Nutrient Pollution and Top Down Control*

While top-down control can attenuate the effects of eutrophication on seagrass ecosystems, nutrient pollution can also influence the strength of top-down control by altering energy distribution in the food web, herbivore feeding patterns, and predator prey dynamics. Eutrophication can increase the strength of top down control either by increasing the actual amount of herbivores or herbivory in seagrass ecosystems, or by reducing the tolerance of seagrasses to such herbivory. For example, as phytoplankton and epiphyte loads increase in response to eutrophication, consumer food supply grows—increasing secondary production in seagrass meadows and energy availability to higher trophic levels. This can lead to increased top down control by herbivores (e.g. Moksnes et al. 2008), which is particularly likely when mesograzers dominate, because their generally short life histories allow for rapid population responses to increased primary production and a potential outpacing of predator control. Because mesograzers and filter feeders generally have a facultative relationship with seagrasses and are capable of consuming large amounts of phytoplankton or epiphytic biomass (e.g. Whalen et al. 2013), this increase in top down control is likely largely facultative. However, in systems where mutualistic mesograzers are rare and most herbivory occurs through larger grazers, eutrophication may still strengthen top down control of these systems even when changes to herbivore population and grazing intensity are minimal. This is because the increased epiphyte loads that generally accompany nutrient pollution increase stress to seagrasses and may reduce their tolerance to direct herbivory. Additionally, increases in secondary production may strengthen non-consumptive predator effects in systems with risk-averse prey and result in less herbivore pressure, as prey in a high energy state are more likely to respond to predation risk (Heithaus et al. 2007). Finally, eutrophication can alter top down control by altering nutrient content or palatability of seagrass and epiphytes. This in turn can influence where, what, and how much herbivores consume.

### *16.4.2 Overexploitation of Consumers*

The most visible effect humanity has on top down control in seagrass ecosystems is actually through removing "the top" of seagrass food webs. Over the past few hundred years, both predators and herbivores have been lost from many coastal ecosystems (Jackson 2001; McCauley et al. 2015). These depletions, which usually target large-bodied consumers like green turtles, sirenians, and large sharks, can eventually lead to depletion of smaller, lower trophic level consumers as old stocks collapse and new target species are harvested (i.e. Pauly et al. 1998). Both depletion of herbivores and predators have important implications for the structure and function of seagrass ecosystems.

Green turtles (*Chelonia mydas*) and dugongs *(Dugong dugon*) have both been subjected to substantial anthropogenic impacts throughout much of their ranges and population sizes are unlikely to approach what they were historically. Industrialized overfishing has also resulted in global population collapse of apex marine predators like large teleosts and sharks, which are disproportionately vulnerable to fishing (Jackson et al. 2001; Myers and Worm 2003; Ferretti et al. 2010). This is of particular concern because of the potential for irreversible losses of apex predator species, as has occurred in earth's terrestrial biomes. The loss of predators large and small alters food web dynamics and can affect herbivore guilds from large bodied megagrazers (Heithaus et al. 2008b, 2014) to amphipod mesograzers (Moksnes et al. 2008) and may alter not only patterns of predation but also reduce important risk effects (e.g. Madin et al. 2016). Shifts in the food web, including species diversity, can also generate or influence trophic cascades that change the strength and direction of top-down control of coastal ecosystems (Jackson 2001; Duffy et al. 2005), leading to overgrazing, increased bioturbation, or plant loss with implications for ecosystem functioning (Atwood et al. 2015). For example, some argue that the ability of mesograzers to facilitate seagrass persistence by consuming harmful epiphytes may been weakened through the loss of apex marine predators, as mesopredators are released from predation and exert further pressure on epiphyte consumers (Williams and Heck 2001), though a trophic cascade may not occur if the mesopredators themselves are omnivores (Heck et al. 2000). Current predator removal studies generally focus on the effects of one or two species interactions, though removal of predators often has cascading effects through multiple pathways simultaneously (Fig. 16.6).

The worldwide plight of shark populations has received considerable attention recently, with population declines estimated to exceed 80–90% in numerous locations (e.g. Baum et al. 2003; Myers et al. 2007; Dulvy et al. 2014; Worm et al. 2013). Although less appreciated, many populations of rays also are threatened (Dulvy et al. 2014), and the potential for rays to generate trophic cascades down the

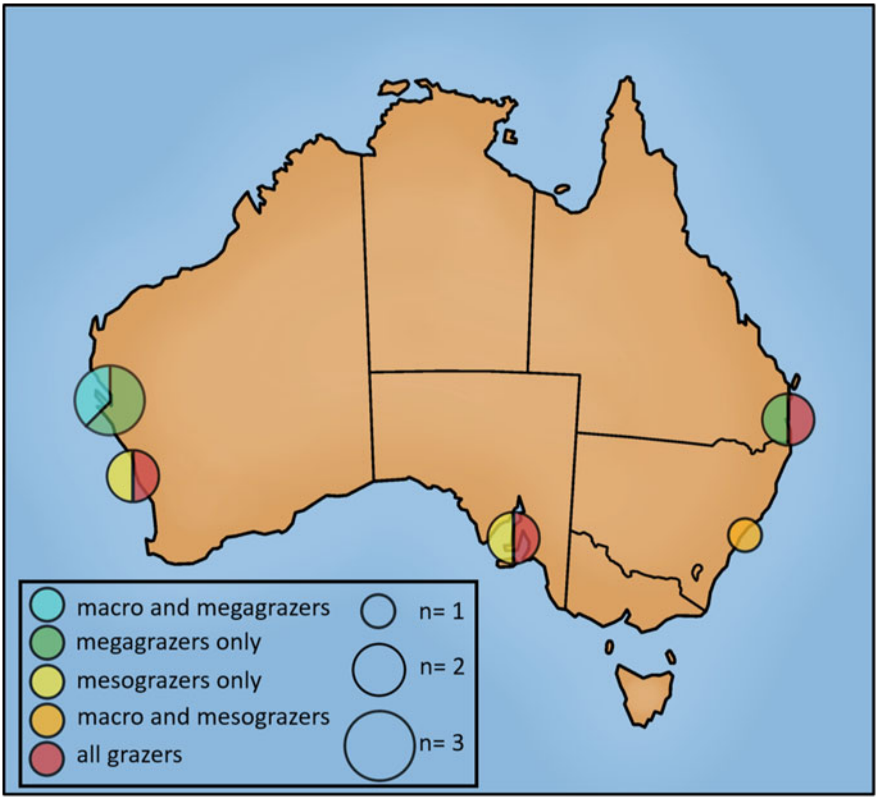

**Fig. 16.6** Map indicating sites of herbivore exclosure field experiments in Australian seagrass ecosystems (Total = 10, n indicates number of studies, some of which include multiple experiments). Studies in yellow achieved herbivore exclusion through in situ chemical pesticide deployments; other studies utilized physical cages; Ebrahim et al. (2014) utilized both. Note a complete lack of exclosure studies in tropical Australian ecosystems. Red studies: Jernakoff and Nielsen (1997), Keuskamp (2004), Ebrahim et al. (2014); orange: Garthwin et al. (2014); yellow: Cook et al. (2011), McSkimming et al. (2015); green: Preen (1995), Masini et al. (2001), Burkholder et al. (2013); teal: Bessey et al. (2016). Note that Ebrahim et al. (2014) performed multiple experiments that varied in level of exclusion, from megaherbivore exclusion only to total herbivore exclusion

filter feeder pathway remains untested. These declines in elasmobranch populations have the potential to modify seagrass ecosystems through multiple mechanisms. Surprisingly, despite the ubiquity of marine apex predator declines and the potential for important consequences to these declines, few studies of the effects of such declines in seagrass ecosystems exist (however see Heithaus et al. 2012 and references therein).

### *16.4.3 Invasive Species*

Seagrasses themselves can be invasive species, though records of this occurring are rare. Successful introductions are exemplified by the recent expansions of two small-bodied, fast-growing seagrasses: *Zostera japonica* along the eastern Pacific Ocean (Mach et al 2014) and *Halophila stipulacea* in the Caribbean Sea (Willette et al 2014). Both of these species have weed-like life history characteristics, including high rates of sexual reproduction and seed set and rapid growth rates that predispose them to be successful invaders. While the documentation of invasive populations of seagrasses into the eastern Pacific and Caribbean is recent, it may be that humans have been spreading palatable, weedy seagrasses around the globe for centuries. Phillips and Menez (1988) have suggested that the weedy, fast-growing species *Halophila decipiens*, widely distributed in harbours across the tropical parts of the Atlantic, Pacific and Indian Oceans as well as some extra-topical locales such as Sydney Harbour, could have been spread by shipping activity. Similarly, *Halophila stipulacea*, originally native to the Red Sea and western Indian Ocean, is proposed to have spread to the Mediterranean sea over a century ago with the opening of the Suez canal before spreading to the Caribbean (Lipkin 1975; Willette et al. 2014). As fast-growing seagrasses are preferred as food over more slow-growing ones, and since the species that natural occur in the regions being colonized by these invaders have slower growth, top-down control by seagrass herbivores may prove to be important in regulating the biomass of these invaders.

Most invasive species in seagrass ecosystems are not seagrass, but algae and fauna (Williams 2007). These invasive species usually generate negative effects in the seagrass ecosystems to which they are introduced (Williams 2007). For example, in San Francisco Bay, USA, the invasive amphipod *Amphithoe valida* consumes *Zostrea. marina* tissues directly in its invaded range (Northeastern Pacific), but rarely consumes *Z. marina* in its native range (the north-west Atlantic) (Reynolds et al. 2012). Additionally, teleost predators in *A. valida*'s invaded range are less effective at controlling its population than predators in its natural range (Carr and Boyer 2014). This highlights not only the importance of understanding herbivore feeding preferences, but also the difficulty in using the ecology of invasive species in their native ranges to predict their effects in their invaded ranges.

Invasive species are likely to become more common in seagrass ecosystems with time, as widespread changes in species distributions occur through both traditional human means (i.e. intentional introduction and hitch-hiking on human transport) and through climate change induced range shifts. These range shifts will be largely poleward and may occur gradually (over decades) or rapidly (over months) (Parmesan and Yohe 2003; Fodrie et al. 2010; Last et al. 2011; Poloczanska et al. 2013; Wernberg et al. 2013; Wernberg et al. 2011a, b; Smale and Wernberg 2013; Vergés et al. 2014). Such shifts have the potential to completely re-arrange communities as species migrate at differing rates. The resulting decoupling of some species-species interactions and the formation of novel ones (Walther et al. 2002; Cheung et al. 2009; Kordas et al. 2011) has the potential to alter the strength of top down control in seagrass ecosystems and to destabilize those ecosystems (Vergés et al. 2014). For example, the herbivorous sea urchin *Centrostephanus rodgersii* has shifted poleward along Australia's southeastern coast by more than 600 km in four decades, resulting in its establishment in Tasmanian waters and a concomitant increase in the prevalence of urchin barrens there; exclosure experiments suggest that *C. rodgersii* is responsible for such barrens, and that community diversity at these sites is reduced by ~70% compared to intact kelp beds (Ling 2008). In the subtropical seagrass habitats of the northern Gulf of Mexico, the tropical herbivorous teleost *Nicholsina usta* has increased in abundance almost 25 fold, and is predicted to reduce seagrass cover as warming continues (Heck et al. 2015). Novel associations between herbivores and predators may also alter the direction of effect of top down control. Despite the global scale at which this community mixing is predicted to occur, we have a poor understand of how new species introductions influence seagrass ecosystems, with the effects of most invasive species unassessed (Williams 2007).

The potential for novel species assemblages to completely restructure benthic marine communities is probably not uniform. Seagrasses in temperate ecosystems are likely more vulnerable than those in tropical and subtropical ecosystems to reorganization of the consumer community. This is because of the higher niche diversity of the tropics, which increases the potential for consumers to exploit previously unoccupied niches in temperate systems (Bennett et al. 2015). Furthermore, tropical seagrass ecosystems will experience fewer introductions via range shifts, since temperature induced range shifts are generally poleward. Conversely, temperate seagrass ecosystems may show recalcitrance to range expansions of tropical seagrasses. Indeed, higher latitudes would reduce available light to tropical species, resulting in both reduced growth rates and potentially increased nutrient content and palatability (Fourqurean et al. 2015). In this sense, range shifts may increase the strength of top down control in temperate seagrass habitats, but via different mechanisms for temperate and tropical seagrasses. Australian seagrass ecosystems will be particularly vulnerable to disruptive distribution shifts as Australia is the only continent to have poleward-flowing boundary currents on both coasts, and because its southern coastline occupies only a narrow latitudinal band—meaning changes in ocean temperatures will have very widespread effects on temperate Australian ecosystems (Wernberg et al. 2011b). This poises Australian seagrass ecosystems on the front lines of climate change and provides both a conservation challenge and an opportunity to study how climate change driven species invasions will alter seagrass ecosystems worldwide.

### *16.4.4 Climate Change*

Climate change is probably the single largest avenue through which humans are altering the marine environment. Most effects of climate change are ultimately due to physical forcing of the environment. However, there is increasing evidence that the ecological effects of climate change will be mediated by biotic interactions (Zarnetske et al. 2012). Beyond altering species distributions, climate change will affect the strength of top down control by altering the metabolism, production and consumption rates of organisms, changing stoichiometric ratios of producers, and amplifying climactic extremes, which may reduce the resilience of seagrass ecosystems to herbivory or other means of top-down control. Understanding how these complex interactions will shape seagrass communities is paramount to the management and conservation of these ecosystems in the era of climate change.

As temperature increases, so do the rates of biological processes of ectotherms such as metabolism and consumption (Hillebrand et al. 2009; O'Connor 2009). This ability of temperature to influence metabolic processes and structure ecosystems is the emphasis of the Metabolic Theory of Ecology, or MTE (Brown et al. 2004). Because changes in temperature have the potential to profoundly alter consumption rates, production rates, and the effects consumers have on their ecosystems, MTE has received an explosive surge in attention in the past decade. Since the overwhelming majority of species in seagrass ecosystems are poikilotherms, such changes in temperature can affect entire communities, though different species are likely to react differently. This is because the relationship between metabolic rate and temperature follows a unimodal pattern that peaks at a species-specific thermal optimum, after which physiological stress weakens the relationship, eventually reducing an organism's fitness (Lemoine and Burkepile 2012). Indeed, a central question in MTE is that of metabolic mismatches: what happens when the metabolisms of different organisms scale differently as temperatures rise? Such differential metabolic scaling can have significant ecological consequences for seagrass ecosystems.

The effects of temperature increases on the strength of top-down control will depend largely on how the metabolisms of producers, herbivores, and predators change in relation to one another. For example, if herbivore consumption rates increase faster than primary producer production rates, then top-down control on plant communities is likely to strengthen. Conversely, increases in predator consumption rates or hunting efficiency may increase top-down control on herbivores, releasing resource species from consumption. Furthermore, rates of primary productivity may outstrip the ability of consumers to regulate it, resulting in a weakening of top-down control. Finally, if temperatures surpass the thermal optimum of a species, fitness may suffer, reducing the interaction strength of a consumer with its prey.

Though the topic of differential metabolic scaling in relation to climate change remains fairly young, multiple examples detailing the effects of simulated or real warming on the strength of top-down control in seagrass ecosystems exist. For example, experimental warming of mesocosms containing amphipod grazers and benthic brown algae *Sargassum filipendula* showed that a 4 °C temperature increase resulted in stronger, more negative per-capita interaction strength between the amphipods and algae, indicating stronger consumer control (O'Connor 2009). Similarly, in mesocosms in the Galapagos Islands, green sea urchins (*Lytechinus semituberculatus)* exposed to multi-day warming (28 °C) doubled their oxygen consumption increased their consumption of the green algae *Ulva* sp. by almost

50% compared to urchins kept at cooler temperatures (14 °C) (Carr and Bruno 2013). In South Australia, when the sea urchin *Amblypneustes pallidus* was placed in microcosms mimicking 5 °C of ocean warming and an increase in $CO^2$ concentrations expected to occur by 2100, urchins increased consumption rates of the Australian endemic seagrass *Amphibolis antarctica* by ~20% (Burnell et al. 2013b). In a predator prey study, experimental warming of a terrestrial old field ecosystem resulted in reduced spatial overlap of spider predators and grasshopper nymph prey, which in turn reduced predator control of herbivores (Barton 2010). In these studies, increases in top-down control were driven primarily by shifts in per-capita effects rather than in consumer densities. This emphasizes the capability of climate change, through physical forcing, to alter the effects of individual consumers on a global scale with potentially significant changes to the strength of top down control at the most basic physiological level.

Climate change may also weaken the potential strength of top-down control by increasing primary productivity. In some cases, this productivity increase can even outpace increased consumption rates of herbivores. For example, experiments in South Australian rocky coastal ecosystems showed that under moderate warming (to 20 °C), the marine gastropod *Turbo undulates* can maintain consumption rates that outpace turf algae production; under conditions predicted by 2100 (24 °C), however, turf algae production outpaced consumption (Mertens et al. 2015). This phenomenon is particularly likely to occur when dominant consumers surpass their thermal optimum and undergo temperature-related physiological stress, reducing their “efficiency” (e.g. Lemoine and Burkepile 2012; Strong 1992), or when grazer control of primary producers is already weak (O’Connor et al. 2009; Eklöf et al. 2012). While compensatory herbivore population growth may dampen runaway productivity effects as consumer populations adjust to reflect the increased food supply, even a temporary loss of consumer control could lead to algal overgrowth of seagrass and increase the likelihood of a regime shift to a seagrass depauperate state, as we will see shortly. Understanding how herbivory, production, predation, and other biological interactions will scale with increases in temperature is critical since seagrass ecosystems are dominated by ectotherms whose metabolism is inherently coupled to ambient temperatures.

While temperature will alter top-down control of consumers, increased $CO_2$ concentrations are predicted to increase seagrass production, since seagrasses are often light and $CO_2$-limited (Borum et al. 2015). However, increased production is often paired with reduced proportions of nitrogen and phosphorous in seagrass tissues, reducing their quality as a food source. For example, six-month $CO_2$ enrichment experiments in South Florida, USA, designed to replicate atmospheric $CO_2$ concentrations in 2100, increased non-structural carbohydrate content of *Thalassia testudinum* rhizomes by 29% but also reduced nitrogen and phosphorous content of leaves by 11 and 21%, respectively (Campbell and Fourqurean 2013). Differences in stoichiometry may increase herbivore consumption rates to compensate for this lower food quality, or may cause herbivores to avoid lower quality plants and switch to plants of higher food quality (Cruz-Rivera and Hay 2001; Valentine and Heck 2001; Russell and Connell 2007; Hillebrand et al. 2009; Tomas et al. 2011). Changes in temperature and ocean chemistry may also alter plant defensive compounds and secondary metabolites. Since consumer preference is driven by a combination of factors which includes plant defensive compounds (e.g. Steele and Valentine 2015), determining whether (and if so, how) $CO_2$ concentrations affect plant defenses will also be a key part in understanding the shifting role of herbivores in top-down control. Multi-species $CO_2$ enrichment experiments should also be undertaken to determine the potential for $CO_2$ enrichment to majorly alter nutrient concentration hierarchies. These experiments should be paired with simultaneous food choice experiments exploring the potential for this to change consumer preferences or herbivory rates. These investigations would be particularly fruitful for Australia's subtropical ecosystems where species and life history diversity of seagrass is highest.

In addition to range shifts, extreme climactic events can alter seagrass communities and potentially increase the ability of top-down control to generate alternate, seagrass-depauperate ecosystem states. Seagrasses ecosystems are vulnerable to regime shifts, whereby the ecosystem tolerates disturbances to a point before rapidly shifting to an alternate ecosystem state that is often resistant to change. Indeed, environmental stress can increase the vulnerability of seagrass to grazing (e.g. Eklöf et al. 2010), potentially resulting in top-down control exacerbating the effects of disturbances after they occur. Regime shifts, initiated by climactic disturbance and reinforced by herbivore control, have already been recorded in Australian marine ecosystems. On temperate algae reefs in Port Gregory, Western Australia, the loss of the algae canopy associated with a marine heat wave (Pearce and Feng 2013) was reinforced by algivorous teleosts, largely tropical in origin (Bennet et al. 2015). This resulted in shift from an ecosystem state dominated by complex canopy forming algae to one of structurally simple turf algae, which was reinforced by constant herbivory on any remaining kelp (Bennet et al. 2015). Shark Bay's seagrass beds, which were subjected to the same marine heat wave (Thompson et al. 2014; Fraser et al. 2014), may be buffered from similar effects as healthy populations of tiger sharks generate antipredator responses in dugongs, minimizing herbivore control of disturbed seagrass beds (Nowicki et al. unpublished data). Australian seagrass ecosystems are particularly susceptible to these interactive effects of climate disturbance and herbivory because both East and West coasts are home to tropical boundary currents that force tropical waters poleward—and while our oceans are expected to warm globally, these "hotspots" are projected to do so 2–3 times faster than average (Wu et al. 2012; Vergés et al. 2014). Furthermore, these currents are capable of generating rapid and extreme warming events (e.g. Pearce and Feng 2013) such as the aforementioned marine heat wave that struck Western Australia in 2011 and caused widespread ecological changes throughout the coast (Wernberg et al. 2013; Smale and Wernberg 2013; Thompson et al. 2014; Fraser et al. 2014). These examples indicate the potential for climactic disturbance and other anthropogenic stressors to interact to alter the role of top-down control in benthic marine ecosystems and highlight the need for a better understanding of how climate change will interact with anthropogenic stressors at regional and local scales (Wernberg et al. 2011a, b).

As our understanding of individual species relationships under climate change becomes clear, it will be necessary to put them in the context of larger, community scale interaction webs if we are ever to elucidate how top down control will change in our warming oceans. Furthermore, we need to consider the potential for temperature induced metabolism shifts to interact with other ecosystem properties to attenuate or magnify the strength of top-down control, especially since few seagrass ecosystems are subject to isolated anthropogenic impacts. For example, nutrient enrichment of producers can result in increased satiation and decreased per capita grazing sea urchins (Valentine and Heck 2001), suggesting that nutrient enrichment may attenuate some effects of temperature induced increases in consumption rates (Burnell et al. 2013b).

## 16.5 Conclusions and Future Directions

### *16.5.1 Progress Since the Last Edition*

In the first edition of this volume, published over twenty five years ago, top down control of seagrass ecosystems was given limited attention focusing on the role of grazing by sea turtles and dugongs, and to a lesser degree, teleosts. This emphasis illustrates an important and relatively unique aspect of Australian seagrass ecosystems: many still have ecologically functional populations of megaherbivores and apex predators, particularly in the tropics and subtropics. However, in the past several decades, our view of top-down control in seagrass ecosystems has changed dramatically. Thanks to advances in theory as well as an increasing number of laboratory, mesocosm, and field experiments around the world over the past quarter century, there has been a shift from descriptive studies (Duarte 1999) to a more process oriented approach in seagrass ecology. This shift has led to a much better understanding of how mesograzers, predators, and food web structure interact with each other and with bottom-up factors to structure seagrass ecosystems. We also better understand how human impacts, particularly eutrophication (Hughes et al. 2004) and apex predator removal (Heithaus et al. 2008a, b; Burkholder et al. 2013) are likely to influence seagrass ecosystems. New promising field approaches developed in Australian seagrass habitats, such as cage-less mesograzer exclusions (Poore et al. 2009) and long term multi-trophic level ecosystem research projects (*sensu* Heithaus et al. 2012), have already provided critical insight into top-down control of these seagrass ecosystems and will enable further refinement of our understanding of top down control of seagrass habitats worldwide.

### 16.5.2 Gaps that Still Remain

Despite the progress made in characterizing top down control in seagrass ecosystems over the last quarter century, many gaps still remain. In particular, the complexity with which top-down control operates in seagrass ecosystems creates new challenges to generalizing top-down control (Valentine and Duffy 2006). We begin with a call to expand the use of manipulative field experiments in Australian seagrass habitats.. This approach is among the most effective in determining how individual or groups of species influence seagrass ecosystems, and when paired with mechanistic studies can provide powerful insight into how top down control operates in these ecosystems. This is particularly true for the dominant and widespread endemic seagrasses in the genera *Posidonia* and *Amphibolis.* Though they are becoming more common, exclosure and enclosure experiments remain under-utilized in testing theory related to top down control, and these experiments remain rare in Australian seagrass habitats when compared to other geographic regions and types of benthic marine ecosystems. For example, out of over 600 herbivore exclusion experiments analyzed by Poore et al. (2012), only 28 studies occurred in seagrass beds, with only 4 of those occurring in Australia (though there have since been others, see Fig. 16.6). All of these studies have occurred in temperate or subtropical seagrass ecosystems. This is probably largely due to the huge logistical challenges associated with completing marine research in these sparsely populated areas. Nonetheless, we believe tropical Australian seagrass ecosystems are understudied and warrant further attention, particularly as seagrass diversity in tropical Australia is high, and our understanding of herbivory in multi-species seagrass beds is still relatively lacking (Lee et al. 2015). Indeed, northern Australia is home to a diverse and expansive tropical seagrass community as well as large populations of macro- and megaherbivores, suggesting herbivory may be an important structuring force in tropical Australian seagrass beds (e.g. Marsh and Lawler 2002; Marsh et al. 2002; Roelofs et al. 2005; André et al. 2005; Sheppard et al. 2008). This is supported by limited evidence from aerial surveys, which indicate that seagrass beds in parts of the Northern Territory and northern Queensland are often heavily scarred from dugong grazing (Roelofs et al. 2005).

As has been emphasized throughout this chapter, understanding herbivore feeding preferences is critical to predicting the nature of top-down control in seagrass ecosystems. A large body of research has investigated relationships between food quality, plant defenses, seagrass structure, and the effects of associated producers, yet these experiments necessarily simplify the number of variables tested due to experimental constraints. We still lack a generalizable mechanistic understanding of how seagrass properties as a whole influence food preferences or consumption rates by herbivores. Instead, we are limited to rough generalizations (such as the previously discussed dichotomy in herbivore feeding preference), which are based on larger patterns from food preference experiments. The relationship between seagrass properties and herbivore feeding behavior is confounded by seagrass properties including palatability (high nutrient, soluble carbohydrate, and lipid content), undesirable traits (defensive phenolic compounds, low nutrient content, and high fiber content), and seagrass structure, which can vary among and within species as well as through space and time. This relationship is further obscured by the variable efficacy of phenolic defenses on different herbivores and the differential perceived value of each of these seagrass properties by different herbivores (e.g. Goecker et al. 2005; Prado and Heck 2011). Because of this it is still difficult to generalize how herbivory influences seagrass community response to anthropogenic stressors like eutrophication and $CO_2$ enrichment, or how pressures on herbivores (such as predation risk) may alter patterns of top-down control. Given the ubiquity of these stressors and the knowledge that they can interact (e.g. Burnell et al. 2013b), pursuit of a predictive model of how this may occur warrants serious attention. Meta-analyses would be useful to determine how patterns of seagrass nutrient concentration, phenolic compounds, carbohydrate content and other characteristics relate to seagrass consumption rates of different herbivores.

Over the past two decades it has become increasingly apparent that grouping consumers into ecological guilds based on taxonomy or size over-simplifies the diversity of their ecological functions (Duffy et al. 2001, 2003; Valentine and Duffy 2006). This is most true for mesograzers. For example, selective herbivore exclusion experiments in Moreton Bay, Queensland, showed that exclusion of small amphipod mesograzers resulted in a more than doubling of epiphyte biomass while exclusion of larger invertebrate mesograzers resulted in increases in seagrass shoot height, density, and cover (Ebrahim et al. 2014). A similar experiment showed that some mesograzers control epiphyte loads while others do not (Jernakoff and Nielsen 1997). Clearly, these organisms have distinct functional roles in top down control yet are generally grouped simply as “mesograzers.” This has been recognized as an oversimplification as ecosystem level impacts are the result of complimentary effects from a diverse range of grazers—not from a single homogenous effect by a uniform herbivore guild (Duffy et al. 2001, 2003; Hughes et al. 2004; Burkepile and Hay 2008; Holzer et al. 2011; Rossini et al. 2014). Yet gaps remain in our understanding of the complimentary roles of sympatric herbivores or the relative strength with which they can exert top-down control (but see Holzer et al. 2011)—often limiting our ability to estimate the net effects of groups of herbivores or herbivores as a whole on seagrass communities. This is an important omission—particularly in regards to differences in interaction strength between major grazer groups and seagrass-because megagrazers, macrograzers and mesograzers are often managed very differently (if at all). Additionally, the effects different grazer groups can generate in seagrass ecosystems can be surprising; for example, herbivores can generate opposite responses in seagrass communities even when they consume the same species of seagrass. Dugongs can facilitate the same seagrass species they target when grazing through destructive and indiscriminant feeding tactics which also remove competitively dominant climax seagrass (Preen 1995). Invertebrate and teleost herbivores, however, are more selective and instead usually suppress the species they target.

Finally, our understanding of how top-down control of seagrass ecosystems will change in the context of human stressors like overfishing and climate change is still in its infancy. Indeed, while there is an increasing focus on how trophic interactions will change as climate change variables continue, few of these studies are in marine ecosystems (Rosenblatt and Schmitz 2014). Furthermore, most of these studies fail to capture the complexity climate change will bring to trophic interactions—often only manipulating two trophic levels and one climate change variable at a time (Rosenblatt and Schmitz 2014). Understanding how climate change, overfishing and other human impacts will alter top down control of seagrass ecosystems will require increasing both the complexity of existing experiments to better understand interactions, and rigorous syntheses of existing experiments to discover general patterns between these factors.

### *16.5.3 Maximizing Research Potential in Australian Seagrass Habitats*

One problem of studying top-down control in coastal ecosystems (including seagrass ecosystems) is that today's seagrass communities have often been fundamentally altered from the conditions under which the ecosystems evolved (Heck and Valentine 2007; Jackson 2001; Dayton et al. 1995). As a result, studies (particularly of predators) in today's seagrass ecosystems probably don't accurately capture the historical importance of top down control. Indeed, while we have a solid understanding of the mechanisms through which trophic cascades can operate, determining the net effects of predator loss on seagrass ecosystems remains difficult because trophic cascades can operate through multiple consumer pathways concurrently (Fig. 16.4) and the relative strength of these pathways remains largely unknown. Many of Australia's seagrass ecosystems, particularly those in the tropical northern and western coasts, remain far from large population centers and provide unique opportunities to study top-down control in relatively pristine seagrass ecosystems. Yet, few of these studies exist. By pursuing the effects of megafauna and apex predators in seagrass ecosystems, focusing on relatively pristine seagrass ecosystems where biodiversity and trophic relationships remain relatively intact, and establishing long-term monitoring projects along the eastern and western coasts where tropical boundary currents will generate "sentinel" ecosystems, in which to study climate change, researchers can leverage the natural capital of Australia's seagrass habitats in ways few other regions can. A better understanding of how predators and megaherbivores structure seagrass ecosystems will become increasingly relevant as populations of megaherbivores like green turtles are restored in regions where they were formally abundant (Heithaus et al. 2014).

The ultimate goal of understanding top down control in seagrass ecosystems is to create a testable framework through which we can make generalizations and predict how top down control will impact those ecosystems. For such a framework to be useful it will have to incorporate theoretical advances as well as a huge compliment of field, laboratory, and observational work to test, validate, and refine it. It will also have to incorporate the role of physical factors (such as temperature and nutrient regimes), species traits (such as species identity and food preferences) and trophic structure (competitive, facilitative, and predator prey relationships) and larger community properties (such as biological and functional diversity). Finally, it will involve understanding the processes that drive the patterns we observe. This is an enormous challenge, but one that will be necessary if we are to effectively generalize patterns we observe in a select few seagrass ecosystems to the many that will need to be managed in the future.

## 16.6 Final Thoughts

A wide body of work over the past few decades has shown that top-down control can be an important (and even dominant) structuring force in seagrass ecosystems. However, the complexity of these interacting ecosystems continues to make broad generalizations about top-down control difficult. Many Australian seagrass ecosystems have unique qualities, driven by seagrass or megafaunal assemblages not widely found elsewhere. General ecological theory, derived from studied worldwide, will continue to provide hypothesis to test the role of top-down control in seagrass—but an understanding of top-down control in Australian seagrass ecosystems will ultimately have to come from work inside Australia. We have learned much since the original realization of the importance of top-down control in seagrass ecosystems.. The challenge now is to understand when top-down control is important in seagrass ecosystems, what factors control its strength and effects on the seagrass community, where feedbacks or interactions between factors are likely to occur, and what impacts anthropogenic alterations to the local and global environment will have on top-down control. Further research into these areas will aid pursuit of the end goal of a general integrative framework of top-down control in seagrass ecosystems.

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# Chapter 17
# Faunal Assemblages of Seagrass Ecosystems

**Paul H. York, Glenn A. Hyndes, Melanie J. Bishop and Richard S. K. Barnes**

**Abstract** Seagrass habitats support diverse animal assemblages and while there has been considerable progress in the study of these fauna over the last few decades, large knowledge gaps remain. There are biases in our knowledge of taxonomic and functional information that favour the temperate regions over the tropics, some seagrass genera over others, shallow habitats compared to deeper meadows and larger animals over smaller ones, with many invertebrate communities poorly described. In many areas of Australia, invertebrate identification to low taxonomic resolution is difficult due to a lack of resources, but new approaches, such as genetic barcoding, may one day surpass traditional methods of classification and overcome this issue. Many studies have demonstrated greater biodiversity of fauna in seagrass compared to adjacent bare habitats with explanations for this ranging from habitat and seascape processes to food availability and trophic interactions. Within seagrass ecosystems, meadows can be highly heterogeneous, and habitat factors such as structural complexity, patch size, edges, gaps and corridors influence associated faunal communities. Broader seascape processes that occur across multiple connected habitats, including seagrass meadows, bare sediments, mangroves, saltmarshes and coral and rocky reefs, influence faunal productivity and/or diversity through the movement of organisms for recruitment and migration, and the transport of detritus and nutrients. The study of seagrass food webs has highlighted the importance of bottom-up processes in shaping the faunal assemblages through assessments of the role of invertebrate prey in influencing the productivity of

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consumer species and manipulative experiments that show prey resources affecting spatial patterns of predators. In addition, top-down consumptive and non-consumptive effects of predators such as their modification of prey behaviour also affect the structure of faunal communities. A large number of natural and anthropogenic perturbations to seagrass meadows influence their resident animals. These disturbances can modify seagrass-associated fauna in several ways; directly where seagrass fauna are more sensitive to perturbation than their seagrass habitat, indirectly through habitat modification, and additionally through interventions that reduce connectivity between habitats that fauna use for part of their life cycle. Animals can also play a significant role in structuring seagrass meadows through processes such as herbivory and bioturbation that can have both positive and negative effects on seagrass habitat.

## 17.1 Introduction

Seagrass meadows are known to provide habitat for highly diverse faunal assemblages consisting of animals from all major phyla with dominant groups including invertebrates such as molluscs, crustaceans, polychaetes through to larger vertebrates such as fishes, birds, turtles and dugong. Seagrasses habitat often supports abundances of animals that are substantially (sometimes orders of magnitudes) higher than adjacent areas of bare sediment. Faunal communities can vary greatly both spatially and temporally. For example, tropical multi-species meadows in northern Australia can support very different animals to largely monospecific meadows in south-eastern Australia (see Fig. 17.1).

This chapter looks at the broad cross-section of faunal assemblages associated with seagrass, however, a greater emphasis is placed on invertebrate assemblages as the roles of larger animals are covered more comprehensively in following chapters on fish and fisheries (Chap. 18—Hyndes et al. 2018 of this volume), and dugong (Chap. 19—Marsh 2018 of this volume), and dugong (Marsh 2016). Where available, examples of faunal patterns and processes in Australian seagrass systems are highlighted, however global patterns are also drawn upon to compare and contrast with Australian systems and to plug knowledge gaps where local case studies are lacking. Ecological processes that structure faunal assemblages in seagrasses are investigated. These include changes in environmental variables along gradients of latitude, depth and from estuarine to marine environments. The effect of habitat is examined from small scale processes such as habitat complexity provided by individual plants and epiphytes to landscape processes such as edge effects and patch size to broader processes of connectivity between other seagrass meadows as well as other important habitats such as saltmarshes, mangroves and reefs. Trophic interactions are also important in seagrass faunal assemblages and both bottom-up processes of resource allocation and top-down processes of predation are discussed. The role of disturbance in altering community structure is also examined by looking at the effects of a variety of different perturbations in seagrass

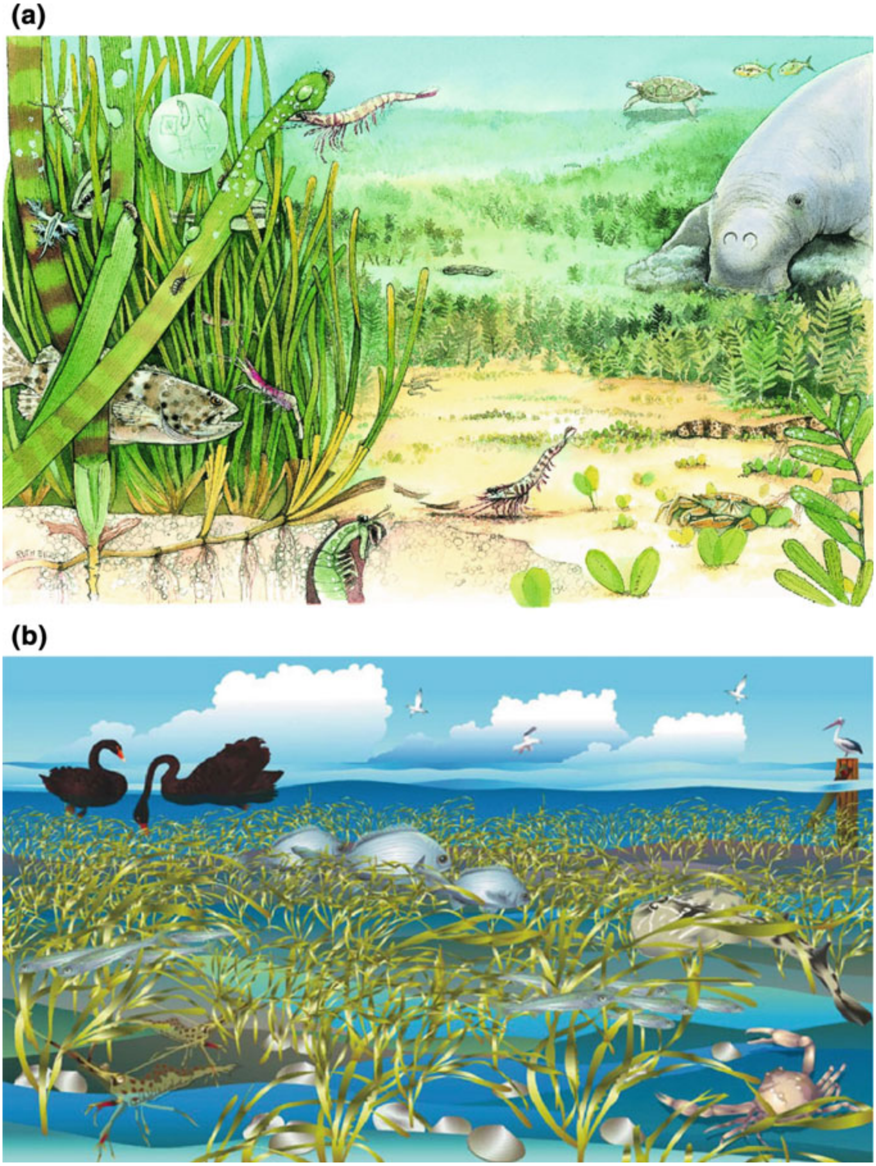

**Fig. 17.1** Artistic impressions of faunal assemblages in **a** tropical seagrass meadows such as found on the Great Barrier Reef showing a multi-species meadow supporting dugong, green turtle, reef fish, and a range of invertebrates such as holothurians, crabs, penaeid prawns and callianassid shrimp and **b** temperate seagrass meadows such as those in coastal Victoria supporting black swans and a variety of shorebirds, banjo sharks and fiddler rays, a variety of estuarine fish including commercial species (black bream and King George whiting) and a variety of invertebrates such as crabs, shrimp and bivalves (Figure **a** was produced by Ruth Berry and provided by TropWATER, James Cook University and figure **b** was provided by the Marine and Freshwater Discovery Centre, Fisheries Victoria)

systems. Finally, not only do seagrass beds structure faunal assemblages but the opposite is also true. The role of animals can also influence the structure of seagrass meadows through herbivory and bioturbation and these processes are discussed. We conclude with a broad summary of how far we have come in the understanding seagrass faunal assemblages over the last few decades and highlight gaps in knowledge that need to be addressed in the future.

## 17.2 Faunal Assemblages

### *17.2.1 Benthic Invertebrate Faunal Assemblages*

Virtually all major groups of invertebrates have been recorded from seagrass meadows, but detailed breakdowns of the relative importance of different groups at different localities are very patchy. For Australia as for elsewhere, more information is available for temperate zones than for the tropics, from the intertidal than for the subtidal, for species of potential commercial importance than for those not, for large species than for the small to very small, and for those associated with the seabed or swimming in the water column than for those living on the seagrass leaves, whether attached to them or moving over them hidden from view by virtue of their minute size. Lack of data from a wide range of sites renders generalization a potentially hazardous exercise but equally a number of species lists from individual well-studied locations will do little to aid appreciation of the rich animal ecology of seagrass (Collett et al. 1984; Edgar et al. 1994; Gibbs et al. 2010, however, all contain lists of macrofauna; Edgar and Robertson 1992; Hutchings 1982; Klumpp and Kwak 2005; Watson et al. 1984; Edgar 1990a, b, 1992).

It is customary to allocate seagrass organisms to a series of categories reflecting their size and where they live. For example, size classes of animals are divided into macrofauna (animals retained by a 500 μm mesh), meiofauna (animals passing through a 500 μm mesh but not 62 μm) and microbenthos (organisms passing through a 62 μm mesh). Animals associated with the seabed are termed "benthic", those suspended in the water column are "planktonic" and larger animals capable of independent movement in the water column are "nektonic". A similar way of categorising fauna that is commonly used for seagrass assemblages is by dividing animals into those living beneath the surface of the sediment called "infauna", animals living on the surface of the sediment or benthic vegetation "epifauna" and swimming animals living close to the sea bed "epibenthic fauna". Epifauna can be divided again into sessile and motile animals. Examples of common taxonomic groups found in these categories are set out below in Table 17.1. Do note, however, that like many of the divisions into which humans attempt to force nature they have very fuzzy boundaries. Several animals, for example, fall into one category during the day or during low tide but into a different one at night or when covered by

**Table 17.1** Major faunal groups associated with seagrass meadows based on their position within the seagrass meadow

| | |
|---|---|
| (i) ***Infaunal*** | **Living beneath the surface of the sediment**<br>*Dominant invertebrate taxa*<br>Harpacticoid copepods, ostracods, nematodes, polychaetes, bivalves, amphipods, cumaceans, holothurians, phoronids |
| (ii) ***Epifaunal*** | **Living on the surface of the sediment or on benthic plants or alga**<br>*Dominant invertebrate taxa—motile*<br>Harpacticoid copepods, ostracods, nematodes, rotifers, amphipods, isopods, small decapods, gastropods, polychaetes, pycnogonids, echinoderms, nemerteans<br>*Dominant invertebrate taxa—sessile*<br>Hydroids, bivalves, bryozoans, sponges, ascidians, serpulid polychaetes |
| (iii) ***Epibenthic*** | **Swimming animals living close to the sea bed**<br>*Dominant invertebrate taxa*<br>Decapods, cephalopods |

water. Some change category from minute to minute, as when fiddler crabs or sentinel crabs pop into and out of their burrow!

Another potentially useful approach of categorising invertebrates is the identification of regularly occurring guilds of species, i.e. groups of species that insofar as we know share a similar ecology particularly with respect to the way in which the seagrass system functions. This classification utilizes a wide range of biological traits such as body size, morphology and capability of movement, diet and feeding location, means of food capture, etc. (see, e.g., Bremner et al. 2003). On such a basis, similar guilds or 'functional groups' seem not only to be present across wide ranges of latitude but, often, to share relative importance. Thus, the functional groups listed in Table 17.2 are the most important numerically of the 24 present along a > 6 km stretch of intertidal seagrass bed on subtropical North Stradbroke Island, Queensland, as well as in the cool-temperate Atlantic and warm-temperate Indian Oceans though not in the same rank order (Barnes and Hendy 2015a).

It is perhaps surprising that the same dominant functional groups should occur across such a wide range of latitude, and it suggests that seagrass comprises a relatively simple system that is capable of supporting up to some 8 or 9 different major functional units as well as maybe up to twice as many minor ones, although any one site is likely to be relatively conducive only to some of these in a rank order of potential favourability, presumably dependent on environmental and structural features of each local area. Local regimes of hydrodynamics, light availability, and even predator-prey dynamics could all influence the relative importance of, for example, suspension versus microphytobenthic feeders, shelled versus unshelled body plans, etc. What is even more surprising is that the proportion of the total assemblage numbers that each functional group comprises is effectively constant across at least small-scale space, e.g. over 0.4 ha (Barnes and Hamylton 2015).

Equivalent functional analyses are not available for the faunal assemblages of other seagrass types, although it is clear that different seagrass genera may

**Table 17.2** The ten most important macrofaunal functional groups of a *Zostera muelleri* bed along the coast of Moreton Bay, with the most characteristic component genera and percentage of the total individuals contained in each

| | |
|---|---|
| 1 | Leaf-biofilm-grazing, epifaunal microgastropod molluscs (esp. *Calopia*, *Pseudoliotia*, *Tricolia* & *Alaba*) (12.7%) |
| 2 | Deposit-feeding, infaunal (tubicolous or burrow-dwelling) worms with ciliated feeding palps, tentacles, etc., that collect food materials from the sediment/water interface (esp. *Prionospio*, *Malacoceros* & *Owenia*) (10.5%) |
| 3 | Omnivorous, free-living peracaridan crustaceans (esp. *Longiflagrum* & *Leptochelia*) (9.1%) |
| 4 | Free-living or burrow-dwelling, subsurface, microbe-, protist- or sediment-ingesting worms (esp. a capitellid & *Armandia*) (6.5%) |
| 5 | Epifaunal predatory/scavenging molluscs (esp. *Nassarius* & *Bedeva*) (6.2%) |
| 6 | Surface-feeding predatory worms (esp. *Onuphis*, *Phyllodoce* & *Amphiporus*) (6.0%) |
| 7 | Omnivorous, free-living decapod crustaceans (esp. *Enigmaplax* & *Diogenes*) (6.0%) |
| 8 | Subsurface-feeding, free-living, infaunal predatory worms (esp. *Goniada* & *Nephtys*) (5.9%) |
| 9 | Sedentary, infaunal, burrow-dwelling or buried, suspension-feeding shell-enclosed species (esp. *Barbatia*, *Mysella* & *Lingula*) (5.8%) |
| 10 | Predatory, free-living peracaridan crustaceans (esp. *Limnoporeia*), consuming small (often meiofaunal) prey (5.6%) |

characteristically support different animals not only because they may typify different environments, e.g. hydrodynamic regimes (Michael et al. 2008), but because of their contrasting forms (Edgar 1990a) and structural complexity (see Gartner et al. 2013) although see Leopardus et al. (2014) for the opposite situation. In deeper areas, amphipod crustaceans of a range of types (suspension-feeders, predators of meiofauna, feeders on algal epiphytes) and larger epifaunally-hunting predatory or microphytobenthic biofilm-grazing crabs living below the surface but feeding at it become more important, for example amphipods comprise 35% of all individuals at a tropical Queensland site (Klumpp and Kwak 2005) and they dominate the epifauna in *Amphibolis* meadows near Perth (Jernakoff and Nielsen 1998).

Large animals are invariably rare whilst small animals may be—though not necessarily are—abundant. The numbers of meiofaunal foraminiferans, nematodes, harpacticoid and ostracod crustaceans can be huge, 5,000 nematodes per 10 cm$^2$ of seagrass-associated sediment, for example (Bell et al. 1984), although "the Australian world of meiofaunal research has hardly been touched" (Coull 1999). Nevertheless, detailed studies on Australian meiofauna have been conducted in Moreton Bay (Walters and Moriarty 1993), Port Phillip Bay (Jenkins et al. 2002; Warry et al. 2009) and along the NSW (Fonseca et al. 2011) and tropical Queensland coasts (Fisher and Sheaves 2003), for example. Evidence suggests that the majority of meiofauna utlilise the same food sources as most of the macrofauna, i.e. microphytobenthos, biofilms and seagrass detritus (Lebreton et al. 2012). Animals also live attached to the seagrass leaves, particularly filter-feeding spirorbid worms, bryozoans, barnacles and ascidians, and carnivorous sea-anemones and hydroids (see, e.g., Prado and Thibaut 2008; Borowitzka et al. 1990; Lemmens et al. 1996), in dense associations which can reduce photosynthetic potential.

Even within the macrofaunal component, small animals have historically been markedly under-represented potentially because of the use of relative large filter mesh-sizes and/or vigorous methods of passing sediment through the sieves. The two most abundant and most widespread macrofaunal species across Queensland's North Stradbroke Island seagrass beds are the micro-gastropod *Calopia imitata* and the micro-brachyuran *Enigmaplax littoralis* (Barnes 2014). Indeed, the <2 mm long *C. imitata* (the largest species in its genus!) is the second most widely distributed snail in the whole of the southern Moreton Bay (Rachello-Dolmen 2013). These snails were unknown before 1999. The taxonomic literature shows the genus to occur from Victoria right up the eastern coast into the Gulf of Carpentaria (Ponder 1999), but ecologically it was first known to be present in Moreton Bay (let alone to be a dominant faunal component) only in 2010 and to date it appears to figure in only one other ecological study (of bare mudflat habitat in Botany Bay—Bishop et al. 2007). Likewise, the <5 mm crab *E. littoralis* was first described only in 1993. If we have only appreciated for the last five or six years that the two animals now known to dominate the macrofauna in the much-studied Stradbroke seagrass beds in the relatively well-known Moreton Bay are there at all, what must our real understanding of other less studied areas be like? Australia is not alone in having this problem, though, the three most common gastropods in South African estuaries all still await generic placement, and one apparently escaped the notice of field biologists for more than a century.

### 17.2.2 Taxonomic Classification of Seagrass Invertebrate Assemblages

The enormous diversity, complex nature and spatial variation in distributions of marine macrofaunal communities coupled with funding challenges and a scarcity of taxonomic expertise to deal with the enormity of the task leaves species assemblages poorly described (Miller 2007; Markmann and Tautz 2005). Traditional morphological techniques of classification are expensive and time consuming and rapid advances in molecular techniques have resulted in new approaches to quantify biodiversity that compliment and may one day overshadow these traditional methods (Bucklin et al. 2011). The phenomenal growth of the use of genetic techniques in ecological studies and the requirement for sequencing data to be made publically available has resulted in libraries of molecular information on a vast and growing number of species in open access databases such as NBCI GenBank (http://www.ncbi.nlm.nih.gov/genbank) and the Barcode of Life Data Systems (BOLD; http://www.boldsystems.org). Individual species or even parts of specimens can now be identified from matching taxonomic signatures from standard DNA regions known as barcodes, (usually from a $\sim$ 648 base-pair region of the mitochondrial cytochrome c oxidase subunit I—(COI) gene) to entries in these public databases. Identification, of course, is currently limited to species that have both already been taxonomically classified and have been assigned a genetic barcode (Aylagas et al. 2014). Species assemblages can now also be analysed using a metabarcoding approach by using a set of primers targeting the phyla of interest (Aylagas et al. 2014). To date, genetic barcoding has been used in seagrass ecology to identify seagrass species in the diet of fish through the analysis of gut contents (Chelsky et al. 2011) and to assess biodiversity in invertebrate assemblages associated with seagrass (Cowart et al. 2015).

### *17.2.3 Neckton: Fish and Large Mobile Invertebrates*

Seagrass beds are well known habitats for fish and large mobile invertebrates, many of which are commercial species (see Chap. 18). Mobile species like fish and large crustaceans use seagrass meadows in different ways (Jackson et al. 2001). Some smaller cryptic species are permanent residents within seagrasses for their entire life (Edgar and Shaw 1995b) while other larger predatory fish use seagrass fish as transient habitat for foraging (Jackson et al. 2001). However the majority of research of fish in seagrass has revolved around the nursery hypothesis, a paradigm that suggests that seagrass habitats shelter assemblages of juvenile fauna which contribute disproportionally to the recruitment of individuals into the adult population (Beck et al. 2001). While direct evidence to support the nursery hypothesis is scant (Nagelkerken et al. 2015), high concentrations of juvenile fish and prawn species are consistently found in Australian seagrass habitats (e.g., Jenkins et al. 1997; Gray et al. 1996) a fact that is often used (mistakenly) to support the hypothesis.

Nekton assemblages in Australian seagrass habitats have generally been well described (e.g., Bloomfield and Gillanders 2005; Guest et al. 2003; Jelbart et al. 2007b; York et al. 2006; Ferrell et al. 1993; Jenkins et al. 1997; Rotherham and West 2002; Hyndes et al. 2003; Middleton et al. 1984). Temperate seagrass fish assemblages are dominated by the families Sygnathidae (pipefish and seahorses), Monacanthidae, (leatherjacket), Labridae (weed whiting and cale), Clinidae (weedfish) and Sparidae (bream and tarwhine) (Kendrick and Hyndes 2003; Smith and Suthers 2000; MacArthur and Hyndes 2001; Wressnig and Booth 2007; Bloomfield and Gillanders 2005), while families, Gobiidae (gobies), Terapontidae (trumpeter), Sillaginidae (whiting) were abundant in both temperate and tropical meadows (Jenkins and Wheatley 1998; Kwak and Klumpp 2004; MacArthur and Hyndes 2007; Smith and Suthers 2000). Tropical regions also supported large numbers from families Leiognathidae (ponyfish), Lethrinidae (emperor) and Lutjanidae (snapper) (Kwak and Klumpp 2004; Coles et al. 1993). Crustaceans, such as some species of penaeid prawns, rely heavily on tropical seagrass meadows as nursery habitat (Haywood et al. 1995; Coles et al. 1993; Loneragan et al. 1998), while temperate meadows are dominated by palaemonid shrimp and portunid crabs (Worthington et al. 1992; Bloomfield and Gillanders 2005).

### *17.2.4 Megafauna: Dugong, Turtles, Waterbirds*

Large fauna are also found in seagrass meadow with assemblages differing across latitudes. Globally, temperate bioregions are dominated by waterfowl and shorebirds. In the northern hemisphere, brent geese, redheads and dabbling ducks are associated with temperate seagrasses and seasonal occurrences and grazing pressure can have significant impacts on the standing crop of meadows (Mitchell et al. 1994; Fox 1996; Rivers and Short 2007). In Australia and New Zealand this role has been exploited by black swans (*Cygnus atratus*), which have been noted as significant grazers of seagrass beds (Choney et al. 2014; Eklof et al. 2009). Studies of seagrass habitat use by shorebirds in Australia are rare, however intertidal seagrass in northern Tasmania have been credited with attracting greater abundances of shorebirds than adjacent habitats to forage on invertebrate prey (Spruzen et al. 2008), and some shorebirds such as the Grey-tailed Tattler are strongly associated with seagrass in Moreton Bay (Thompson 1998).

In sub-tropical and tropical meadows across northern Australia the dugong (*Dugong dugon*) is an obligate feeder of seagrasses and therefore intricately linked with this habitat (Marsh et al. 2011). For more information on dugong see Chap. 19 in this book. Sea turtles particularly the green sea turtle (*Chelonia mydas*) also feed on seagrass and are closely associated with tropical and sub-tropical seagrass beds. Tiger sharks also use seagrass habitat for foraging where they patrol along the shallow edges of meadows to prey on turtles and dugong (Heithaus et al. 2002, 2006).

## 17.3 Patterns of Biodiversity

### *17.3.1 Seagrass Versus Bare Sediment*

It has been known for decades that benthic macrofaunal assemblages may be denser and more species rich within seagrass beds than in adjacent unvegetated sediment, and this has been demonstrated in Western Australia (Edgar 1990a), South Australia (Connolly 1997), Victoria (Edgar et al. 1994), and Queensland (Barnes and Barnes 2012) (see Fig. 17.2). The effect is seen even in relatively open systems of small seagrasses such as *Halophila* (Casares and Creed 2008) and meiofaunal communities in NSW are also known to differ across the two states (Fonseca et al. 2011). Transitions from one habitat type to the other can be very sharp, occurring

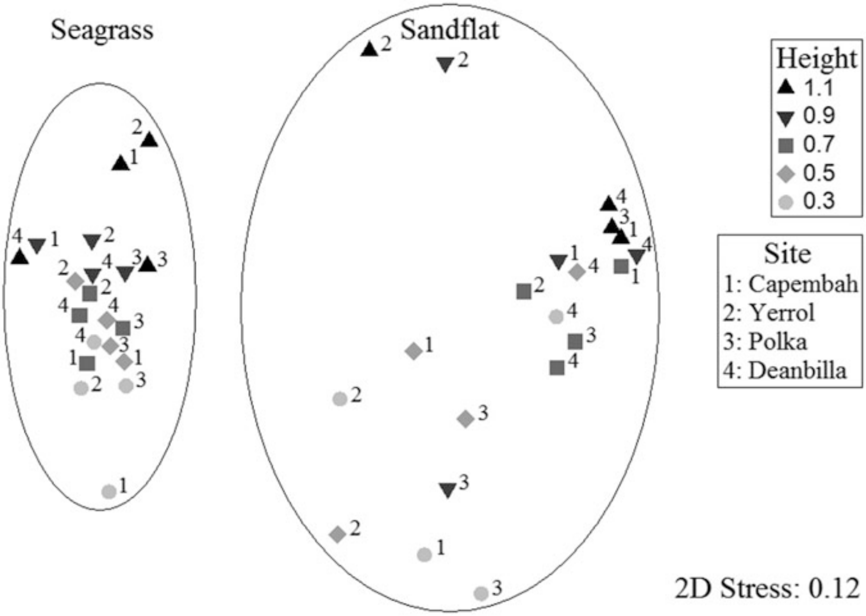

**Fig. 17.2** Marked differences between the macrofaunal assemblages of adjacent seagrass and bare sandflat on North Stradbroke Island, Queensland: nMDS plot of comparisons at four sites, each site with samples from five tidal heights. From Barnes and Barnes (2012). Envelopes are 10% Bray-Curtis similarity; heights are in metres above datum (MLW = 0.55 m). Note also the effect of shore height within each habitat type

within 0.5 m (Fig. 17.3). This has given rise to fears that the current widespread global loss of seagrass (Waycott et al. 2009) will result in affected areas being reduced to states of lesser abundance and biodiversity as a result. Many potential explanations for this effect have been advanced, most based on the notion that seagrass is a more favourable habitat for macrofauna, for example because it may reduce the foraging efficiency of predators and thereby provide a refuge for prey species, or because it can provide greater levels of food availability and of habitat stability and complexity. Nevertheless, this differential is in fact by no means observed universally. Similar seagrass/bare-sediment systems in the North Sea (Asmus and Asmus 2000), New Zealand (van Houte-Howes et al. 2004) and in South Africa (Barnes and Barnes 2014a) either do not show the effect or even display the converse, and it has been suggested that the differences may result, where they do occur, not from any supposed special advantages of the seagrass habitat but from particular unfavourability of those bare sediments structured by bioturbating callianassids and other equivalent destabilizers of the sediment. When the bioturbators are absent, the bare sediment can be as rich or richer than the seagrass, the leaf-biofilm grazing micro-gastropods, for example, now grazing sediment-associated biofilms instead, which without seagrass shading can be

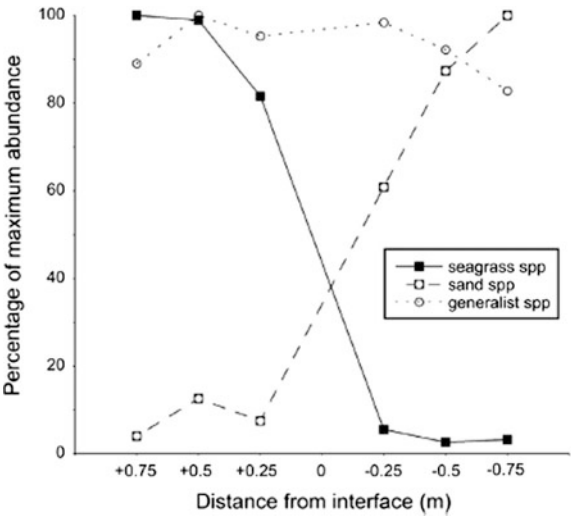

**Fig. 17.3** Transition from the seagrass (+) to the bare-sediment (−) state on North Stradbroke Island, Queensland: percentage of maximum total abundance of seagrass specialist (n = 55), bare-sand specialist (n = 10) and generalist (n = 8) macrofaunal species in each sampling horizon on either side of the interface. From Barnes and Hamylton (2013)

especially productive. Studies in Gulf St Vincent, SA, have shown that carbon originating from seagrass can be traced in unvegetated sediments and in their fauna several hundreds of metres away from the beds (Connolly et al. 2005a), although in southwestern Australia this may be significant only for harpacticoid copepods (Hyndes and Lavery 2005).

### *17.3.2 Are Macrofaunal Assemblages at Carrying Capacity?*

Faunal densities vary widely between locations. Edgar (1990b), for example, recorded densities of just the mobile epifaunal component in *Amphibolis* at Cliff Head and Seven Mile Beach in Western Australia exceeding 125,000 $m^{-2}$ and suggests that food limitation and diffuse exploitative competition are prevalent. In contrast, the mobile epifauna and infauna on North Stradbroke Island do not achieve 3,000 $m^{-2}$ (Barnes 2014). That site (together with the cool-temperate Atlantic and warm-temperate Indian Ocean ones referred to above) show the counter-intuitive feature that the number of such species per unit area, even down to areas as small as 0.0275 $m^2$, are statistically constant across wide areas (at 22.7 ± 0.65 at the Australian site, and a similar value of 20.7 ± 0.40 per 0.0275 $m^2$ in South Africa). These species densities do not depart from those to be expected from the overall frequency of occurrence of members of the species pool under conditions of random assortment (Barnes and Barnes 2014b), which in turn suggests that those assemblages are held well below carrying capacity and that individual species do not influence the distributions or others.

### *17.3.3 Effects of Environmental Variables, Including Those Associated with Estuaries*

The effects of a range of environmental variables on shallow-water and intertidal faunal assemblages have received considerable attention in Australia and elsewhere, although few have specifically concerned seagrass faunas. A number of studies, however, have investigated the effect of shore height on the diversity and density of seagrass-associated animals. It might appear self-evident that increasing elevation would have a marked influence on the distribution of marine animals, and such has been reported from experimental studies at various sites in NSW (Nicastro and Bishop 2013). But all is not quite as straight-forward as it might appear, in that although natural variation in assemblage composition did occur upshore on North Stradbroke Island, Queensland (Barnes and Barnes 2012: see Fig. 17.2), there were no significant changes in overall assemblage metrics, and few have been found at Knysna in South Africa either (Barnes and Ellwood 2011). This is likely to be, in part at least, consequent on the seagrass cover retaining high water content within and over the surface of the sediment during low tide. Animals may be insulated from tidal changes.

Another environmental feature likely a priori to influence seagrass faunas is the upstream gradient in estuaries, along which the dwarf-eelgrasses (*Zostera*) in particular can penetrate into very low salinities. Surveying 48 Tasmanian estuaries, Edgar and Barrett (2002) concluded that at low-tidal and subtidal levels, species richness, faunal biomass and estimated productivity were all highly correlated with both salinity and seagrass (and other macrophyte) biomass, whereas faunal density was highly correlated only with seagrass biomass. But relationships between environmental and biological variables were poorly defined at high tidal levels. Collett et al. (1984), surveying the *Posidonia* beds in five NSW estuaries, also found a clear distinction between marine and estuarine faunal assemblages, with, not surprisingly, deposit feeders dominating the relatively muddy estuarine seagrasses whereas suspension feeders and herbivores were most characteristic of marine sites. These feeding categories are very broad, however, and using a more detailed functional-group approach on the seagrass-associated macrofauna up the Knysna estuarine system in South Africa, Barnes and Hendy (2015b) showed that although species diversity and species numbers fell upstream, the major functional groups present were little affected by the salinity gradient. All occurred virtually throughout the system, although the average number of species within individual functional groups decreased upstream. In all, a wide range of responses of individual functional groups was shown (Fig. 17.4). The same is likely to be true elsewhere, and all but one of the groups shown in Fig. 17.4 also characterise Australian seagrass systems. The exception, the biofilm-grazing starfish *Parvulastra exigua* does indeed occur in Australia, but whereas in South Africa it occurs both on seagrass leaves under sheltered lagoon-like conditions, it is much more common in rockpools, in Australia. There they can “graze up to 60% of the epilithic micro-algae beneath their everted stomach during a single feeding event

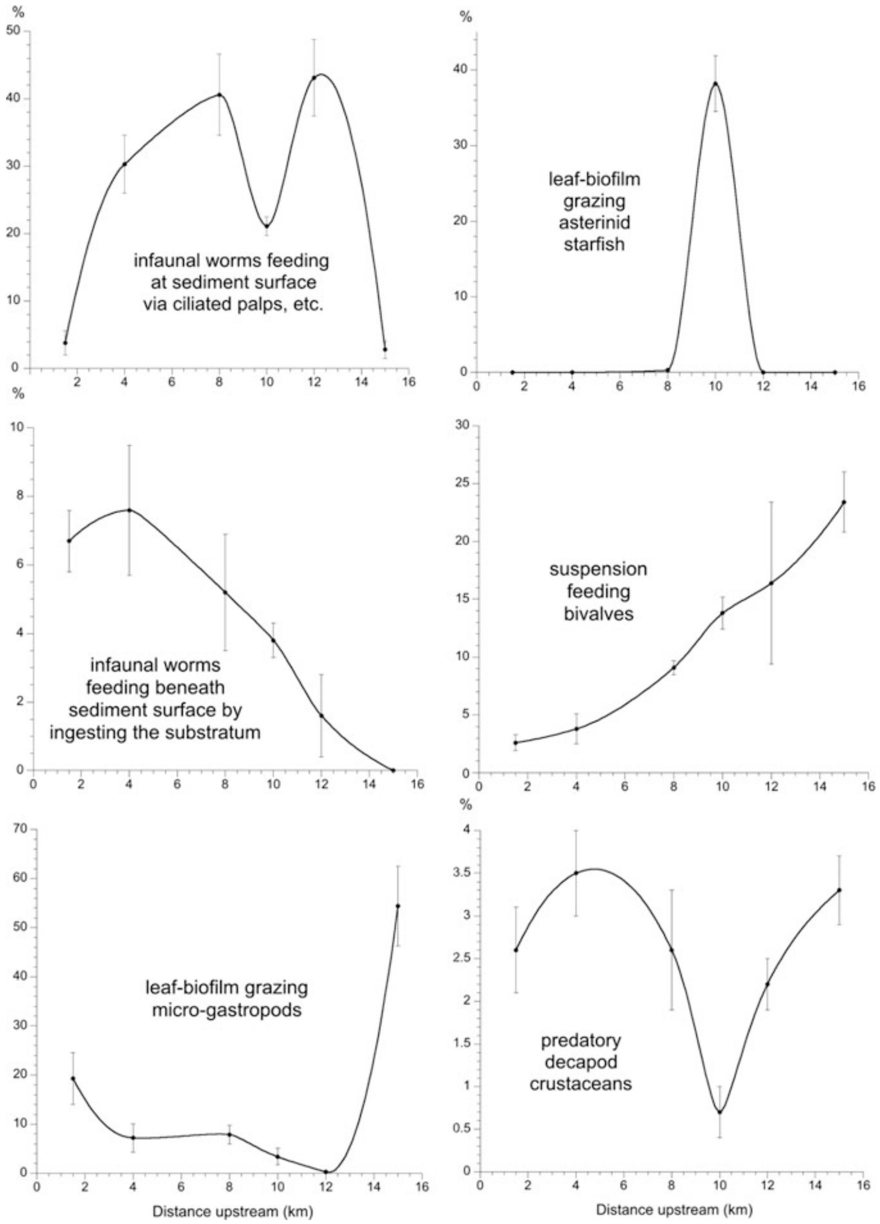

**Fig. 17.4** Percentage importance of various functional groups of seagrass-associated macrofauna along an estuarine system (the Knysna estuarine system, South Africa). From Barnes and Hendy (2015b)

lasting on average 22 min. Over 5 days, two caged starfish could remove nearly half of the available micro-algae from areas of 144 cm$^2$." (Jackson et al. 2009). Why they don't also digest the epiphytes from seagrass leaves in Australia is not known.

## 17.4 Landscape Processes

Interest in understanding seascape processes across a range of scales has increased dramatically over the last 2–3 decades, no doubt due to: (1) a broader acceptance that individual habitats are not isolated units but rather interconnected through various processes (Boström et al. 2006; Hyndes et al. 2014; Polis et al. 1997); and (2) the large losses of seagrass throughout the world (Waycott et al. 2009). Seascape processes occur across multiple habitats and spatial scales, where movement of organisms through recruitment and migration, and transport of detritus and nutrients through water movement can influence the productivity and/or diversity in a mosaic of habitats (Polis et al. 1997; Hyndes et al. 2014). Seagrass meadows are often part of a mosaic of coastal habitats including unvegetated sediments, mangroves, saltmarshes and coral and rocky reefs (Bloomfield and Gillanders 2005; Lugendo et al. 2006; Grober-Dunsmore et al. 2007; Nagelkerken et al. 2008; Tuya et al. 2010). Even within seagrass ecosystems, meadows can be highly heterogeneous, and associated fauna may be influenced by seascape factors, such as structural complexity, patch size, edges, gaps and corridors (Boström et al. 2006). Here, we discuss the influence of various seascape factors and connectivity processes that can influence seagrass assemblages.

### *17.4.1 Habitat Complexity*

At very local spatial scales, differences in plant morphology and cover which result in varying levels of habitat complexity are thought to play a part in structuring the faunal communities associated with seagrass habitats. It is often hypothesised that increased habitat complexity provides a greater number of niches for animals to occupy, therefore resulting in increased species richness and abundance of fauna (Heck and Wetstone 1977). Structural variables such as leaf density, canopy height, leaf morphology, branching structure, and the amount of epiphytes on leaves have been shown to affect faunal abundances (Edgar and Robertson 1992; Gartner et al. 2010; McCloskey and Unsworth 2015; Gartner et al. 2013; Jenkins et al. 2002). However, others such as Attrill et al. (2000) have argued that structural complexity is not a major driver of invertebrate assemblages and those patterns of faunal abundance and richness are best explained by the amount of seagrass (biomass) at a location in a simple species—area relationship. It is generally accepted that a combination of mechanisms such as shelter, food resources and protection from predation are the major drivers of change in faunal diversity and abundance associated with varying levels of habitat structure or abundance, although the strength of the roles played by each of these mechanisms may vary among habitats and species and are not well understood (Parker et al. 2001; Gartner et al. 2010, 2013).

### *17.4.2 Edge, Patch Size and Fragmentation*

Heterogeneity of seagrass habitats is often examined in terms of patch size and edge effects, which are influenced by environmental factors and seagrass species (Boström et al. 2006). Interest in understanding the influence of these seascape attributes on seagrass fauna has coincided with increased fragmentation and loss of these habitats over the last few decades (Connolly and Hindell 2006; Boström et al. 2006). Results from studies of edge effects and patch size vary among faunal groups. Greater abundances of epifaunal crustaceans (amphipods, isopods, grass shrimp and tanaids) have been recorded within 0.25–1 m of seagrass edges compared to meadow interiors in a study by Tanner (2005), however, few infaunal polychaete or bivalve species responded in the same way. Another study of zooplankton and meiofauna also found variable results with some animals increasing in abundance around the habitat edge (e.g., cumaceans), some declining at seagrass edges and into unvegetated habitat (e.g., copepods and amphipods) while others (crustacean nauplii and bivalve larvae) increased moving across the meadow edge and into bare sand (Macreadie et al. 2010a). Studies of edge effects and patch size in larger, more mobile species like fish have also produced variable and contrary results, and often no relationships are found (Connolly and Hindell 2006). This is likely to reflect over-riding influences of other environmental factors, species identity or sampling design issues (Connolly and Hindell 2006), with the latter highlighting the need to adopt appropriate approaches to determine patch size and effects (Bell et al. 2001). Comparisons of species richness between seagrass edges and interiors in *Zostera muelleri* beds of different sizes found more fish species in meadow interiors when patch size was sufficiently large, however, this relationship did not hold in smaller patches which have uniform richness equivalent to those in the interior of larger meadows (Jelbart et al. 2006). In contrast, a study in Port Phillip Bay found greater abundances of fish at the seaward edge of meadows compared to the middle and the shoreward edge, although patterns of abundance varied among species (Smith et al. 2008).

It must be recognised that fragmentation is a process, while variables such as patch size and edge effects that are described in many studies reflect static states that may represent a particular phase in fragmentation. For example, Warry et al. (2009) showed that while the dominant meiofauna (harpacticoid copepods) in artificial seagrass units showed greater abundances at edges in stable patchy and continuous habitats, edge effects disappeared during the process of fragmentation. Macreadie et al. (2010b), also using manipulative experiments with artificial seagrass units, found greater abundances of fish and crustaceans in habitats undergoing loss compared to habitats that were stable in size or increasing in area. These results were short-lived, lasting a matter of days and were attributed to the crowding of animals as habitats shrunk (Macreadie et al. 2010b).

### *17.4.3 Cross-Habitat Movement of Nekton*

Seagrass meadows are often adjacent to other habitats, such reefs, in a mosaic of coastal habitats across the seascape scale. Movement of water and nekton provide mechanisms of connectivity that can strongly influence productivity and diversity (Hyndes et al. 2014). Numerous species of decapods and fish undergo diel or tidal movements across habitats (Krumme 2009), and many studies on fish in habitat mosaics in tropical systems indicate that migration of fish into seagrass meadows is related to foraging excursions (e.g., Nagelkerken and van der Velde 2004; Grober-Dunsmore et al. 2007; Nagelkerken et al. 2008; Olds et al. 2012; Unsworth et al. 2008; see Chap. 18 for more detail). Foraging movements of predators and herbivores, which often seek shelter in the highly structured reef habitats, can alter both seagrasses and their epiphytes and faunal assemblages, particularly at the edges of seagrass meadows. For example, herbivorous urchins and fishes using reef habitats as shelter can create halos of bare patches in surrounding seagrass meadows (Nagelkerken et al. 2000; Ogden et al. 1973), while predators can reduce abundances of seagrass-associated prey (e.g., Tuya et al. 2010; Verweij et al. 2006).

Despite evidence of foraging movements across habitats in Australia (e.g., Verges et al. 2011; Welsh and Bellwood 2012; Marnane and Bellwood 2002), studies examining such movements and their effects on neighbouring habitats in the region are limited. Due to the concerted research effort on the economically important western rock lobster, *Panulirus cygnus*, this species provides the most complete example of cross-habitat foraging movements of fauna in an Australian seagrass system. Juvenile lobsters occur in a mosaic of habitats in south-western Australia, where they occupy caves and ledges in limestone reefs during the day, and undergo nocturnal foraging excursions into adjacent seagrass meadows (mainly *Posidonia* and *Amphibolis* species), unvegetated sand or flat-reef pavement habitats (MacArthur et al. 2008; Jernakoff 1987; Cobb 1981). Lobsters are omnivorous, feeding on invertebrates and macroalgae including seagrass epiphytes (Edgar 1990c; Jernakoff et al. 1993; MacArthur et al. 2011). The species has been shown through experiments to reduce the densities of the gastropod *Cantharidus lepidus* (Edgar 1990e). Based on the concentration of foraging mainly within 60 m of the reef at Boullanger Island (MacArthur et al. 2008; Fig. 17.5), the impact of this lobster is focused at the edges of the seagrass meadows. Indeed, lower densities of this prey species near the reef likely reflects foraging by lobsters and fish moving into seagrass meadows (Tuya et al. 2010).

A habitat's influence on the productivity and biodiversity of neighbouring habitats will depend on complex interactions between movement and foraging

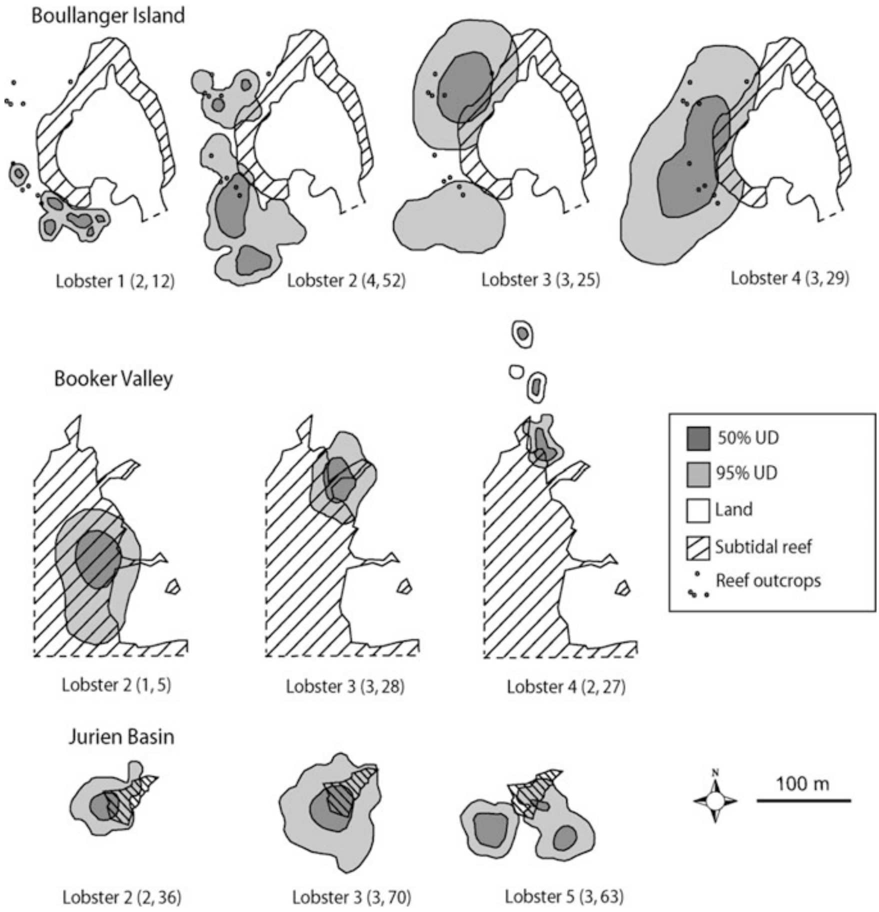

**Fig. 17.5** 95% (total) and 50% (core) fixed kernel Utilisation Distributions (UD) for lobster tracked at Boullanger Island, Booker Valley and Jurien Basin between February and April 2007 using data combined over all nights. Numbers in parentheses are number of nights tracked then number of position estimates. From Macarthur et al. (2008)

activities of predators or grazers, recruitment processes of propagules, and species identity. In south-western Australia, predatory fish are more abundant in close proximity to reef, but predation rates on crabs did not reflect this pattern (Vanderklift et al. 2007). In contrast, predation pressure was greater near the reefs for two grazing gastropod species in the seagrass meadows in similar locations (Tuya et al. 2010; Fig. 17.6). Predation is higher however for *C. lepidus* than *Pyrene bidentata* (Tuya et al. 2010), which appears to reflect the ability of the lobster *P. cygnus* (and possibly predatory fish) to consume this gastropod because of its more fragile shell compared to *P. bidentata* (Tuya et al. 2010; Edgar 1990e). Furthermore, recruitment of *P. bidentata* close to the reef appears to counteract the

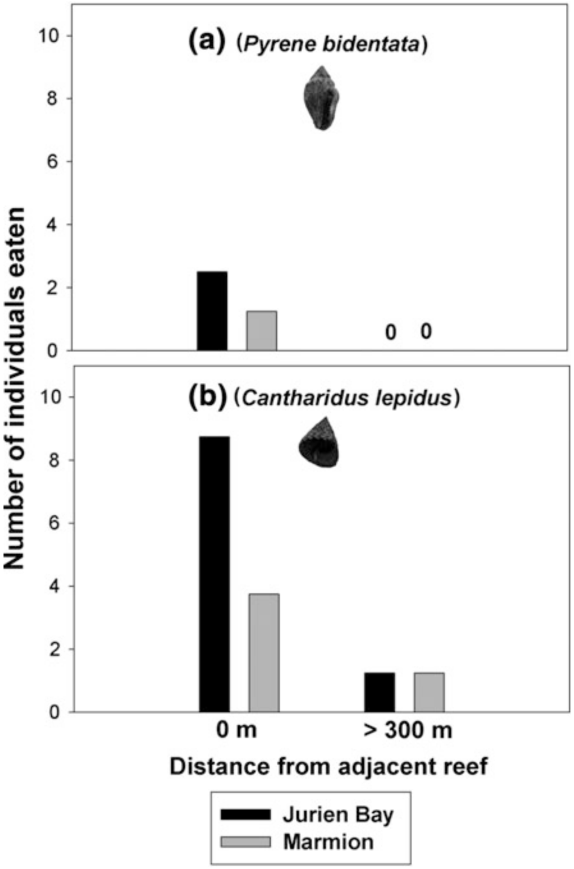

**Fig. 17.6** Relative intensity of predation (number of gastropods eaten during 5 days, n = 20) on *P. bidentata* and *C. lepidus* in seagrass meadows at different distances from adjacent reefs. From Tuya et al. (2010)

effects of predation, whereas *C. lepidus* recruit throughout the meadow but predation pressure reduces its densities near the reef (Tuya et al. 2010; Fig. 17.7). Thus, while these two gastropod species display similar dietary preferences for seagrass resources (Doropoulos et al. 2009), species identity plays a major role in predation pressure on this functional group. Similarly, different grazing crustaceans can play a similar functional role in *Zostera* meadows in north-eastern USA, but different roles as food resources for higher trophic levels (Duffy et al. 2001).

The movement of nekton into and out of seagrass meadows provides an important mechanism for seagrass nutrients to be transported to other habitats. These movements can range from small-scale foraging movements from adjacent habitats, to large-scale ontogenetic movements from nursery habitats to offshore spawning areas (Fig. 17.8b). Ontogenetic movements are based on the larvae recruiting into benthic habitats (Adams and Ebersole 2009), including seagrass "nursery" habitats where they can benefit from high growth rates and survival (Heck Jr. and Valentine 2006). The juveniles can then subsequently undergo an offshore migration to their spawning grounds. Through a stable isotope approach,

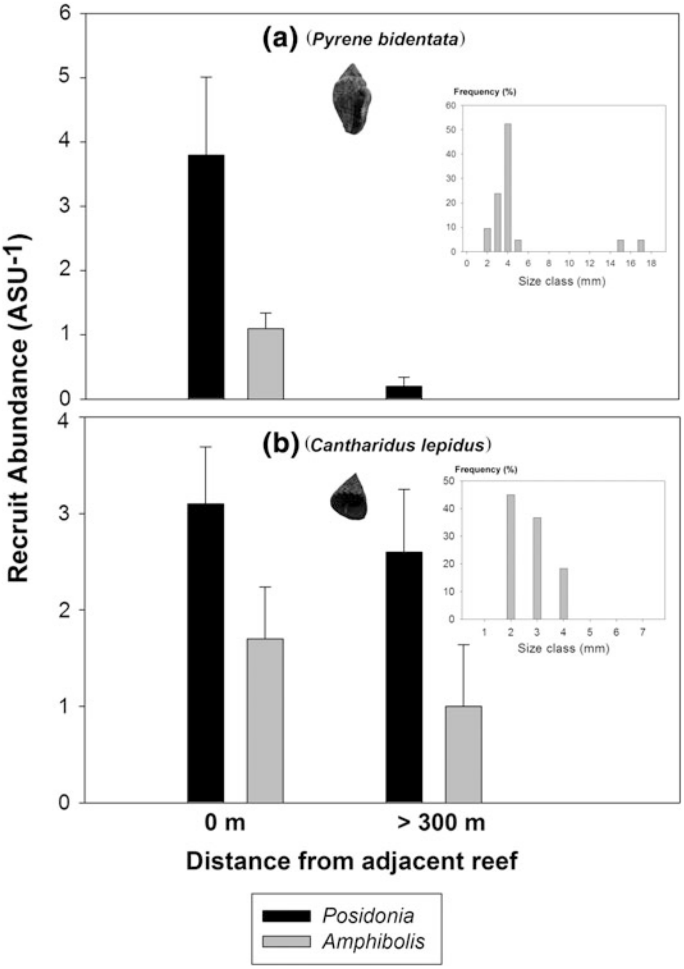

**Fig. 17.7** Abundances (mean + SE, n = 10) of recruits of *P. bidentata* and *C. lepidus* in Artificial Seaweed Units placed in seagrass meadows at different distances from adjacent reefs dominated by either *Amphibolis* or *Posidonia*. Inserted: size-class distributions (total body whorl, data pooled from both seagrass meadows). From Tuya et al. (2010)

Fry et al. (1999) showed that juvenile pink shrimp, *Farfantepenaeus duorarum*, from seagrass meadows in the USA contributed substantially to the fishery in offshore unvegetated areas. Similarly, seagrasses and/or their epiphytes contribute to the production of juvenile prawns (*Penaeus* species) in a tropical Australian estuary, and subsequently contribute to the offshore fishery in the region (Loneragan et al. 1997). Such an ontogenetic movement from seagrass meadows to spawning grounds also occurs for a range of fish species, including the King George whiting *Sillaginodes punctatus* (see Chap. 18).

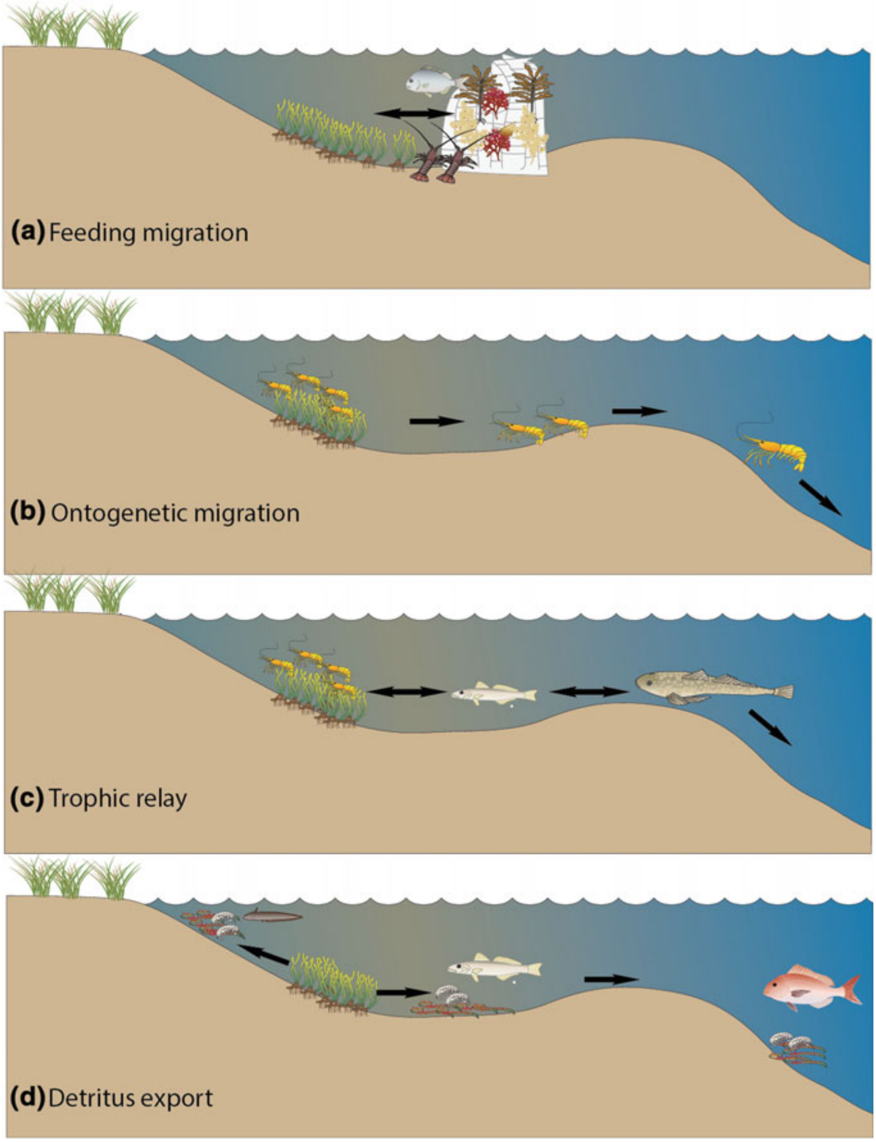

**Fig. 17.8** Conceptual diagram of the four main mechanisms for flow of organic matter from seagrass meadows to fish in other habitats: **a** feeding migration of nekton; **b** ontogenetic migration of nekton; **c** trophic relay through nekton; and **d** detritus export increasing secondary production in other habitats

The movement of juvenile nekton from seagrass to other habitats can also result in a "trophic relay" (sensu Kneib 1997), based on the predator-prey interactions and the sequential offshore shifts in the series of prey and predator species (Fig. 17.8c). This process was first described by Kneib (1997) for saltmarsh systems. While there are no clear examples of this process in seagrass systems, the concept would be equally relevant for those systems. Using saltmarsh as an example, the glassfish *Ambassis jacksoniensis* migrates into tropical saltmarshes on north-eastern Australia, where it consumes large quantities of shore crab larvae (Hollingsworth and Connolly 2006). Their emigration from the saltmarshes and subsequent predation by larger fish would result in a trophic relay (Bouillon and Connolly 2009). Since seagrass meadows provide important "nursery" habitats for numerous nekton (Heck et al. 2003), trophic relays are likely to be initiated through the movement of juveniles out of seagrass meadows and their subsequent consumption by predators. Quantitative data on this process are lacking in seagrass habitats providing a fruitful area for future research.

### *17.4.4 Cross-Habitat Movement of Detritus and Nutrients*

The transport of organic matter from a productive (donor) habitat to a less productive (recipient) habitat can result in enhanced productivity and diversity in the recipient system. This process has been termed a "spatial subsidy" (Polis et al. 1997), and appears to be important in a range of coastal habitats (Hyndes et al. 2014). Seagrass meadows can act as both a recipient and donor habitat. Due to the baffling effect of seagrass leaves, detritus from the water column can settle out into the habitat and drive the food web (Cebrian 2002). Because of this ability to trap particles from the water column, as well as retain detritus from within the habitat, seagrass meadows are often considered to have detritus-driven food webs (Cebrian 2002). While biomarker approaches, including stable isotopes and fatty acids, are now commonly used to examine food web structure in coastal habitats (Connolly et al. 2005b; Fry et al. 1999; Smit et al. 2005, 2006; Crawley et al. 2007), ambiguity in the biomarker signatures among several algal food sources (Hanson et al. 2010) often makes it is difficult to determine whether the sources driving food webs within these systems are internally or externally derived. As a consequence, studies can often only speculate that allochthonous algal food sources contribute to productivity within seagrass meadows (Smit et al. 2005, 2006; Belicka et al. 2012). However, through manipulating the stable isotope signatures of the kelp *Ecklonia radiatia*, which deposits into seagrass meadows from nearby reefs in south-western Australia (Wernberg et al. 2006), Hyndes et al. (2012) were able to show that nutrients for this allochthonous kelp could be taken up by grazing gastropods or by seagrasses and their epiphytes. These gastropods feed equally on either autochthonous epiphytic algae or allochthonous kelp (Doropoulos et al. 2009), indicating that inputs of kelp could increase food availability for the grazers, which in turn appears to increase their densities and biomass (A. Cartraud, unpublished data). Whether this subsidy is evident in other seagrass systems is yet to be shown, but this process of connectivity in seagrass systems needs to be examined further.

Export of detritus from seagrass meadows to other habitats forms another process of connectivity (Fig. 17.8d). Seagrass meadows are productive systems that export on average 15% of their production, although the proportion exported varies markedly among regions and seagrass species (Heck et al. 2008). The spatial scale of its influence ranges from unvegetated areas adjacent to the meadows, through to shoreline habitats and deep-sea habitats. Deposition rates in most of those habitats are unknown, but vary from 140 to over 2000 kg $m^{-2}$ $year^{-1}$ of seagrass and macroalgae deposits on beaches worldwide (Hyndes et al. 2014), where this material known as "wrack" is often obvious. Mateo (2010) estimated that 7% of seagrass production is deposited on beaches in Spain, while Kirkman and Kendrick (1997) estimated almost 20% of seagrass and kelp production deposited on beaches in south-western Australia. Clearly, the export of this material has the potential to influence productivity in other habitats, although studies on this role are limited for most habitats.

Through the export of detritus, seagrasses and their epiphytes are thought to form important base food sources for a range of fish species in nearby mud flats in tropical Australia, but the level of their contribution varied among fish species (Melville and Connolly 2005). Similarly, *Posidonia* meadows in southern Australia have been shown to either directly or indirectly support the production in unvegetated mudflats adjacent to seagrass meadows, including polychaetes and shrimp (Connolly et al. 2005a), and the whiting *Sillago schomburgkii* via invertebrate prey (Connolly et al. 2005b; Belicka et al. 2012). However, Hyndes and Lavery (2005) showed that *Posidonia* detritus contributed little to the food web of adjacent unvegetated sand areas in south-western Australia. These conflicting results suggest that the flow of detrital seagrass through the food web of adjacent habitats may vary with region or species identities.

Despite seagrass detritus forming a large part of the accumulations of wrack in surf zones and on beaches (Hyndes et al. 2014; Colombini et al. 2003), there is limited evidence of its direct flow to higher trophic levels in these habitats (Hyndes et al. 2014). South-western Australia provides a useful case study to examine the role of seagrass in beach-line habitats, as a large amount of work has been carried out in this region. Surf-zone wrack in the region provides an important habitat for invertebrates and fish. The amphipod *Allorchestes compressa* is the dominant invertebrate, which provides an important food source for a range of fish species, including the cobbler *Cnidoglanis macrocephalus* and the trumpeter *Pelsartia humeralis* (Crawley et al. 2006; 2009; Lenanton et al. 1982). However, in contrast to macroalgae such as kelp, seagrass provides a limited role as either habitat or food for the mesograzing amphipod in the surf zone (Crawley and Hyndes 2007; Crawley et al. 2009).

Seagrass does, however, appear to play a greater role as habitat and food source for semi-terrestrial and terrestrial invertebrates on the beach (Ince et al. 2007; Mellbrand et al. 2011). With limited direct grazing on seagrass leaves, the flow of seagrass into higher levels is likely to rely on bacterial decomposition and leakage of dissolved organic nutrients. Large quantities of dissolved organic carbon (DOC) are released from freshly removed seagrass leaves, but the release rate decreases exponentially with time, and the bacterial community associated with the DOC display a similar pattern (Lavery et al. 2013). Bacteria have been estimated to account for ~90% of production in wrack on South African beaches (Koop and Griffiths 1982), but this is likely to be associated with kelp's dominance in the wrack. The research in south-western Australia suggest that the dominant seagrasses in the region (*Posidonia* and *Amphibolis* species) provide a trophic dead-end in the surf zone, but the physical breakdown of this organic matter is likely to provide a mechanism for the further release of nutrients and uptake by bacteria and marine primary producers. Furthermore, different chemical characteristics and decomposition and grazing rates of different seagrass genera (Belicka et al. 2012) suggests that the nutrients of other seagrasses may flow more readily to higher trophic levels. This is clearly a research area worthy of greater effort.

We know very little about the role that seagrass plays in offshore areas, despite evidence that seagrass detritus can occur in submarine canyons and off the continental shelf in some regions (Josselyn et al. 1983; Thresher et al. 1992; Suchanek et al. 1985). Echinoderm species in deep-sea areas of the Caribbean appear to consume seagrass detritus from shallow coastal areas (Suchanek et al. 1985), while production of larval blue grenadier, *Macruonus novaezelandiae,* in the offshore waters of south-eastern Australia appears to be supported through a microbial pathway by the influx of coastal seagrass detritus (Thresher et al. 1992). It is likely that significant amounts of seagrass detritus accumulate in other offshore and deep-sea areas, where it is likely to contribute to secondary production, but needs to be confirmed.

## 17.5 Trophic Structuring

### *17.5.1 Bottom up Forces—Resource Provision*

As primary producers, seagrasses have the potential to exert "bottom-up" control on faunal communities by determining the total amount of energy that enters the system. Studies manipulating the productivity of seagrass have been used to examine the extent to which the structure of faunal communities is driven by this energy flow. In nutrient-poor, oligotrophic, systems such as those that typify south-eastern Australia (Scanes et al. 2007), nitrogen and/or phosphorus is limiting of seagrass and/or epiphytic algal growth (e.g., Kelaher et al. 2013; Udy and Dennison 1997; Udy et al. 1999; York et al. 2012; Bulthuis et al. 1992). In these systems, nutrient enrichment experiments can be used to enhance the productivity of seagrasses and test the importance of bottom-up control (e.g., York et al. 2012; Kelaher et al. 2013).

In oligotrophic estuaries of temperate and sub-tropical Australia, seagrass growth and the standing biomass of seagrass and epiphytes is typically enhanced in nutrient enriched as compared to unenriched control plots (e.g., Kelaher et al. 2013; Udy and Dennison 1997; Udy et al. 1999; York et al. 2012). Although few epifaunal and nektonic species directly consume seagrass, an increase in seagrass biomass in some instances benefits grazers by increasing the surface area available for establishment of epiphytes, the biomass of which is also enhanced by nutrient enrichment (Kelaher et al. 2013; York et al. 2012). In some instances, the resulting increase in grazer biomass also leads to enhancement of predator biomass (Kelaher et al. 2013), although effects on this trophic group may be difficult to detect at locations where there is human extraction of fish (York et al. 2012 See Fig. 17.9).

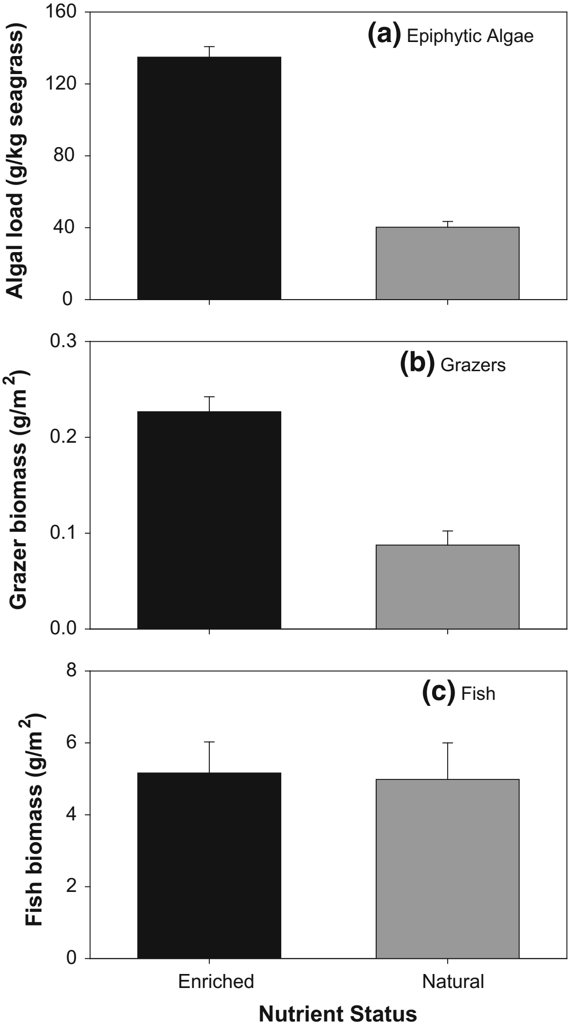

**Fig. 17.9** Bottom up effects of nutrient enrichment from catchment development. Coastal sites in central New South Wales surrounded by developed catchments and with seagrass beds that were enriched with nitrogen had significantly greater loads of **a** epiphytic algae compared to seagrasses in sites surrounded by undeveloped catchments. These enriched sites also contained **b** greater biomass of grazing invertebrates (predominately amphipods and gastropods) indicating an upwardly cascading effect of resource. This effect was attenuated at the level of **c** juvenile fish which prey on the grazing invertebrates and showed no difference between enriched and ambient nutrient sites

The importance of bottom-up processes in shaping the faunal assemblages of seagrass beds is supported by studies assessing the role of invertebrate prey in influencing the productivity of consumer species. Calculations of rates of prey consumption relative to rates of prey production are suggestive that availability of high quality crustacean prey may limit the production of fishes in seagrass habitats (Edgar and Shaw 1995a). Furthermore, experiments directly manipulating prey resources within seagrass beds also lend support to the importance of bottom-up processes in influencing spatial patterns of predators (Macreadie et al. 2010c). Through resource supplementation experiments, Macreadie et al. (2010c) were able to demonstrate that the greater abundances of pipefish, *Stigmatopora argus*, at the edge than the interior of seagrass patches is directly driven by the abundance of crustacean prey items.

Where seagrass and epiphyte growth is enhanced by nutrient enrichment, resource availability for detrital pathways may also be increased (Kelaher et al. 2013). In most Australian seagrass beds (with a few exceptions in northern Australia, where dugongs are present), grazing pressure on seagrass is low (e.g., Wressnig and Booth 2008; White et al. 2011). For these beds, most seagrass production enters detrital pathways (e.g., Bishop and Kelaher 2007). Seagrass detritus may directly contribute to the biomass of invertebrates such as prawns (Loneragan et al. 1997), although relative to algal resources its detritus is relatively refractory (Smit et al. 2006). In instances where epiphytic growth is not controlled by grazers (e.g., Poore et al. 2009; but see Verhoeven et al. 2012), it too may serve as an important carbon source for seagrass food webs (Smit et al. 2006).

In addition to providing autochthonous organic matter through their carbon fixing, seagrass beds may also trap allochthonous organic matter. The structure of seagrass shoots can slow currents (Peterson et al. 2004), resulting in deposition of particulate organic material and detritus from a diversity of aquatic and terrestrial sources (Kennedy et al. 2010). Stable isotope analyses indicate that as much as 50% of carbon in seagrass sediments may be from allochthonous sources (Kennedy et al. 2010) and comparisons of organic matter accumulation below artificial seagrass units and control plots also supports a structural role for seagrass in trapping allochthonous organic matter (Nicastro and Bishop 2013). This allochthonous carbon may modify benthic invertebrate communities by determining the availability of food resources for deposit-feeding infauna (Nicastro and Bishop 2013).

### *17.5.2 Top Down Forces—Predation*

In addition to an enhanced abundance of food resources, a weakening of top-down predator control by the structural complexity of seagrass is a hypothesis commonly put forward to explain the greater abundance and richness of invertebrates and small fishes inside than outside of seagrass beds (Heck and Thoman 1981). For many herbivores, detritivores and mesopredators, predation is an important source of mortality. Where the structure of seagrass reduces predator density, predator-prey encounter or detection rates, enhanced survivorship of prey may occur inside seagrass patches as compared to in adjacent habitats. In addition to these consumptive effects of predation, the structure of faunal communities of seagrass may also be affected through non-consumptive effects of predators such as their modification of prey behaviour and habitat selection.

In Australian seagrass landscapes, the role of predation in shaping faunal communities has been addressed using four main approaches. First, spatial surveys of known predators of seagrass-dwelling fauna and their prey have been conducted, testing the hypotheses that these will be more abundant in sand than seagrass patches, and negatively correlated with prey abundances. Second, tethering experiments have been conducted, comparing rates of predation on prey species of interest inside versus outside of seagrass patches. Third, seagrass density has been manipulated in the absence and presence of predators, testing the hypothesis that the effects of seagrass removal will be stronger when predators are present than absent. While the first two of these approaches have greatly enhanced our understanding of how predators and predation vary in space, the third, manipulative, approach is required to establish causation between predators and faunal communities of seagrass. Studies have primarily focused on the role of predators in shaping epifaunal and nekton communities, with relatively little research assessing the importance of predation in determining the infaunal communities of seagrass (but see Gribben and Wright 2014). Additionally the relative importance of consumptive versus non-consumptive effects has not been addressed.

Observations of predator foraging behaviour (e.g., Heithaus 2005; Heithaus et al. 2002; Smith et al. 2011; Zharikov and Skilleter 2002) and, in some instances also gut content analyses (e.g., Klumpp and Nichols 1983; Edgar 1990c, d; Edgar and Shaw 1995a) have revealed that predators of faunal communities of seagrasses may include fish, crabs, whelks and birds. For some, such as shorebirds foraging on sand and mudflats at low tide, seagrass patches do not represent a barrier to movement (Zharikov and Skilleter 2002). For others, such as large predatory fishes foraging in subtidal landscapes, the complex structure of seagrass may block or impede movement, resulting in predator densities that are lower inside versus outside of seagrass beds (Smith et al. 2011). The decreasing cost of underwater video cameras has facilitated studies examining variation in subtidal predator abundances across small spatial scales. Through deployment of video cameras, inside seagrass beds, at the seagrass-sand interface and in sand patches close to and away from seagrasses, Smith et al. (2011) were able to document spatial variation in the abundance of Australian salmon, a key predator of many small fish within seagrass beds (Robertson 1982; Hindell et al. 2000b). Salmon spent more time over sand adjacent to seagrass than other positions and were linked to the predation and distribution of King George whiting recruits, and, pipefish predation (Smith et al. 2011).

Tethering experiments are suggestive of spatial variation in predation across seagrass landscapes, but do not always produce results that are consistent with patterns of prey species abundance. For example, in Port Phillip Bay, Victoria, the increasing survival time of tethered pipefish from sand habitats, to seagrass patch edges to seagrass patch interiors was not consistent with the greater abundance of pipefish at the edge than the interior of seagrass patches (Smith et al. 2008; Macreadie et al. 2009). Hence, pipefish may balance the enhanced predation pressure at patch edges with factors that maximise energy uptake and/or growth at patch edges (Orth et al. 1984).

Manipulative experiments have also provided mixed evidence for a role for predators in influencing the faunal communities of Australian seagrass. In Botany Bay, Bell and Westoby (1986) found that reducing the density of seagrass had the same negative effect on the abundance of six prey species found in seagrass irrespective of whether predators were present or absent. Instead, small prey migrated through predator-exclusion mesh to more favourable habitats. A larger-scale experiment in Port Phillip Bay revealed that despite consistently greater abundances of nekton and epifauna inside than outside of seagrass patches, exclusion of predators from patchy seagrass habitat only led to patterns of enhancement of faunal abundances that were consistent with an effect of predators at some sites (Hindell et al. 2001). In predator enclosure experiments, enhancement of the abundance of juvenile *Arripis truttacea*, which feed voraciously on early post-settlement fishes (Hindell et al. 2000b), had similar negative effects on the abundance of small fish and atherinids in seagrass and unvegetated habitats (Hindell et al. 2000a). Of the taxa examined, the only one for which abundances were less negatively influenced by predators in seagrass than unvegetated habitat were the syngnathids (Hindell et al. 2000b). In aquarium experiments, Kenyon et al. (1995) found that the ability of sand bass *Psammoperca waigiensis* to detect and capture juvenile tiger prawns *Penaeus esculentus* was reduced in seagrass as compared to bare habitat, and was reduced in broad-leafed as compared to narrow-leafed seagrass.

Although it is usually assumed that predator-prey interactions will decline linearly with increasing seagrass density, this may not be the case where other abiotic conditions that alter predator or prey behaviour also co-vary. On an intertidal sandflat of Tasmania, the proportion of the dominant clam, *Katelysia scalarina*, that buried deeply (as opposed to shallowly) in sediments declined with seagrass density (Gribben and Wright 2014). This behaviour, which was possibly a consequence of greater sediment redox potential at high seagrass density, greatly enhanced susceptibility to predation. As a consequence, densities of clams did not increase linearly with seagrass density, but instead displayed a non-linear pattern of greatest density at 33% cover (Gribben and Wright 2014).

### 17.5.3 Amelioration of Other Biotic and Abiotic Stressors

In addition to offering protection from predators, and enhancing the availability of food resources, amelioration of competitive interactions among species and of abiotic stressors may be among the mechanisms by which seagrass beds support dense and diverse faunal communities.

Seagrasses may ameliorate intra- and inter-specific competitive interactions among fauna by enhancing the availability of substratum for attachment, by reducing the incidence of interference interactions among mobile species and by increasing the availability of food resources. The abundance of many sessile marine invertebrates is limited by the availability of hard substrate for attachment, with competition for space intense (Connell 1983; Dayton 1971). Similarly, in nursery habitats in which species densities are high, interference competition can limit densities and growth rates of mobile species such as crabs (Moksnes 2004). Where competitive interactions are important in structuring populations, increasing densities or surface areas of seagrass blades may be expected to enhance faunal abundances and/or growth rates by weakening competitive interactions. By providing a greater surface area for growth of biofilms, increasing densities and surface areas of seagrass blades may also reduce the intense competition among gastropod grazers for algal spores, which is often experienced on hard substrates (Underwood 1984). Studies manipulating the surface area of seagrass blades using artificial seagrass units have demonstrated that the abundance of epifauna increases with total shoot surface area (Lee et al. 2001) and it is likely that a reduction in competition for space and food resources is a major driver of this pattern. Surprisingly, however, experiments that include the necessary manipulations of faunal density and seagrass to demonstrate amelioration of competitive interactions by seagrass have not been attempted in Australian systems, or elsewhere.

Likewise, the role of seagrass beds in ameliorating abiotic stressors has received relatively little attention, anywhere in the world. Seagrasses may, potentially, alter microclimate as a consequence of the canopy shading the substratum below, and, where they are found in the intertidal zone, by enhancing moisture retention of sediments at low tide. In seagrass beds, irradiance 20 cm below the seagrass canopy can be 34–90% lower than at its surface (Enriquez and Pantoja-Reyes 2005). This self-shading has been demonstrated to influence the architecture of seagrass beds (Enriquez and Pantoja-Reyes 2005), but it is unclear how it directly influences faunal communities, particularly in the intertidal zone where it has the potential to ameliorate temperature and desiccation stress at low tide (Peterson 1991). Similarly, although the capacity of seagrass beds to reduce wave energy has been demonstrated across a range of species (Fonseca and Cahalan 1992), it is unclear how this reduction in energy influences the structure of seagrass faunal communities.

Carefully designed manipulative studies are needed to confirm that the structure of seagrass indeed plays an important role in ameliorating abiotic and biotic stress.

## 17.6 Effects of Disturbance on Seagrass Fauna

Seagrass beds and their resident fauna are subjected to a large number of natural and anthropogenic perturbations such as cyclones, floods, wave action, dredging, anchoring, propeller scars, trampling, storms, bait digging as well as pollution events (e.g., Preen 1995; Reed and Hovel 2006; Skilleter et al. 2005; Walker et al. 1989; West 2012; Short and Wyllie-Echeverria 1996). Disturbances that fragment seagrass meadows, change the density or traits of their shoots and roots, or alter their productivity may modify faunal communities by changing their habitat (Reed and Hovel 2006; Fig. 17.10a). In addition to these indirect effects of perturbations on seagrass fauna, direct effects may occur where seagrass faunas are more sensitive to perturbation than their seagrass habitat (Figs. 17.10b, c). Additionally, where fauna spend only part of their life cycle associated with seagrass beds or move between habitat patches to forage, interventions, such as the construction of flood gates, revetments, and dams may influence seagrass fauna by reducing connectivity (Fig. 17.10d).

It is often assumed that the effects of nutrient loading are detrimental to seagrass ecosystems and the faunal communities they support. In nutrient-rich, eutrophic systems, nutrient addition can have large negative indirect effects on seagrass fauna by stimulating fast-growing algae that may overgrow and kill seagrass (e.g., Silberstein et al. 1986; Cambridge et al. 1986) or decompose in seagrass sediments, reducing components of the infauna (Cummins et al. 2004). Additionally, where excess nitrogen uptake causes carbon-limitation of seagrass, nutrient addition may cause structural weaknesses to seagrass and result in direct lethal effects that influence the habitat available to fauna (e.g., Burkholder et al. 1994, 1992). Experimental nutrient enrichments in eastern and southern Australia have, however, revealed that at oligotrophic locations, nutrients can have positive indirect effects on fauna by increasing the abundance of seagrass epiphytes that provide food and habitat to small epifauna such as amphipods (Morris et al. 2007).

Although studies have separately examined how physical disturbance (e.g., Skilleter et al. 2006, 2007) and features of the seagrass seascape influence faunal communities (e.g., Bell and Westoby 1986; Jelbart et al. 2006), few have coupled the two to disentangle the mechanisms by which disturbance impacts faunal communities of Australian seagrass beds. Physical disturbances to seagrass sediments, such as bait-digging, boat propellers, mooring chain scars, and dugong grazing, may directly modify the infaunal communities of seagrass beds through burial, but also indirectly influence these communities by modifying the structure of seagrass beds and sediment characteristics such as granulometry, compaction, and stability (Skilleter et al. 2006, 2007). Skilleter et al. (2007) found that up to 85% fewer animals were found in dugong trails as compared to adjacent ungrazed areas. The positive relationship between root density and the abundance of several taxa, suggested that removal of seagrass was at least partially responsible. Other taxa, such as amphipods, however, displayed reductions in abundance in areas of dugong grazing that were not correlated with losses of seagrass structure, suggesting that other mechanisms, such as the physical disturbance of sediments, were also at play.

Pollutants, such as metals, may have toxic effects on seagrass fauna that act independently of their effects on seagrass (Fig. 17.10b). Sampling of faunal communities of seagrass beds situated at various distances from a lead smelter in Port Pirie, South Australia revealed that 20 vagile species of fish and crustacean displayed linear or non-linear negative relations to concentrations of Cd, Cu, Mn, Pb or Zn in seagrass sediments (Ward and Young 1982). Field acute toxicity tests demonstrated causation between particular metals and reduced abundances of several, but not all, taxa (Ward 1984).

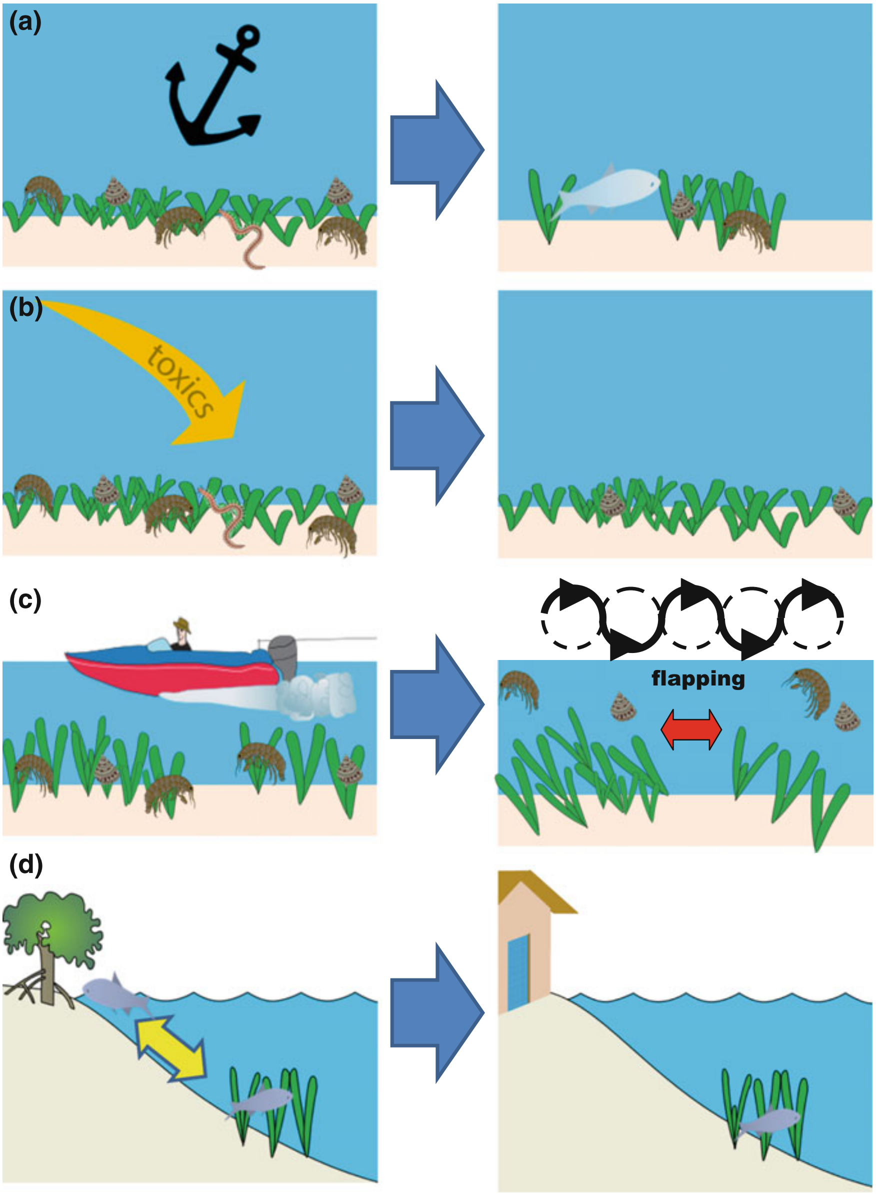

**Fig. 17.10** Conceptual model of how different disturbances can affect seagrass faunal assemblages: **a** small scale physical disturbance from anchor damage and propeller scars; **b** input of toxic contaminants; **c** physical disturbance from boat wakes and; **d** catchment development affecting connectivity with adjacent habitats

Similarly, wave action may have direct effects on faunal assemblages of seagrass (Moran et al. 2003; Bishop 2008) that occur independently of any indirect effect arising from fragmentation of chronically exposed seagrass beds (Fonseca and Bell 1998; Fig. 17.10c). The oscillating flow of waves causes seagrass blades to flap back and forward (Ghisalberti and Nepf 2002; Grizzle et al. 1996; Koch and Gust 1999; Ackerman and Okubo 1993). The resulting movement may resuspend small fish (Moran et al. 2003) and produce lift and drag forces that challenge the attachment strength of invertebrates living on seagrass blades (Bishop 2005). In Port Phillip Bay, the abundance of post-larval fishes and pipefish generally increased in the plankton and decreased in seagrass beds during periods of high wave action, presumably due to resuspension (Moran et al. 2003). In a sheltered northern Sydney lagoon, exposure of *Zostera muelleri* seagrass beds to boat wake resulted in reductions in epifaunal invertebrate abundance and richness that persisted for over an hour following exposure (Bishop 2008).

Although studies have examined how the process of fragmentation leads to changes in faunal communities by altering patch morphology (Bell and Westoby 1986; Jelbart et al. 2006; Macreadie et al. 2009), the effect of perturbations that modify connectivity among seagrass beds or between seagrass beds and adjacent habitats have not been examined. As outlined above, in Australian estuaries, fish and invertebrates may move from seagrass habitats to mangrove and saltmarsh habitats to forage during spring high tides (Saintilan et al. 2007), such that faunal assemblages in seagrass beds proximate to mangrove forests differ to those found in those further from mangroves (Skilleter et al. 2005; Jelbart et al. 2007a). Disturbances, such as dredging, construction of groynes and breakwaters, which modify circulation patterns may alter connectivity among seagrass patches and between seagrass patches and adjacent patches. Additionally, where disturbances modify the landscape context of seagrass beds by altering the structure and function of adjacent habitats, changes to the faunal communities of seagrass beds may also be expected (Fig. 17.10d).

## 17.7 Faunal Processes Structuring Seagrass Ecosystems

While we have demonstrated the many ways that seagrass attributes and landscapes can structure faunal communities, it is also true that animals can play a significant role in structuring seagrass meadows through processes such as herbivory and bioturbation.

### *17.7.1 Herbivory*

The structure of seagrass habitats can be shaped by grazing of herbivorous fauna. Grazing in seagrass systems can occur either indirectly by removing epiphytes growing on the seagrass leaves or by the direct consumption of seagrass material. Globally, greater attention has been paid to indirect grazing by small invertebrates (e.g. amphipods, isopods and gastropods) on epiphytes and the positive effect on seagrass systems by reducing competition for light and enhancing seagrasses photosynthesis (Douglass et al. 2007; Jaschinski and Sommer 2008). Grazers have often been credited with providing a balancing force against increased epiphyte growth caused by nutrient enrichment of coastal systems by catchment development (Hughes et al. 2004). Herbivory of epiphytes by mesograzers in Australian meadows has been shown to increase the growth of seagrass shoots (e.g., Verhoeven et al. 2012) and also increase abundance (Ebrahim et al. 2014). Direct grazing on seagrasses has generally been thought to be quite low, at approximately 6% of net primary production (NPP) in temperate meadows, however this increases to approximately 26% in tropical meadows with the presence of megaherbivores (Hyndes et al. 2014).

Direct herbivory occurs from a wide variety of fauna and can have positive, negative or neutral effects on seagrass habitat. While there is a conventional paradigm suggesting small mesograzing crustaceans and gastropods feed primarily on epiphytic algae, new studies are also highlighting direct grazing on and damage to seagrass that has previously been underestimated (Rossini et al. 2014). Larger invertebrates such as urchins have been known to induce substantial localised losses of biomass after grazing events (Langdon et al. 2011; Burnell et al. 2013). Grazing by fish has been observed in temperate seagrass systems by species such as garfish (Waltham and Connolly 2006; Edgar and Shaw 1995a), leatherjacket (Wressnig and Booth 2008), and zebra fish, cale and weed whiting (White et al. 2011; MacArthur and Hyndes 2007). Generally, the levels of biomass removal by fish in these systems, is seen as low compared to the overall standing stock available (White et al. 2011; Wressnig and Booth 2008). In the tropics however, grazing pulses by herbivorous fish such as parrot fish can outstrip production leading to a reduction in biomass (Unsworth et al. 2007). The effects of fish grazing are generally higher in marine protected areas where fishing is restricted (Alcoverro and Mariani 2004).

Direct herbivory by megaherbivores is also thought to be greater in the tropics with the presence of dugong and turtles. In subtropical areas with large dugong and turtle populations it has been hypothesised that constant grazing pressure can favour rapidly growing colonising species such as *Halophila ovalis* over slower growing foundation species such as *Zostera muelleri* (Preen 1995; Kuiper-Linley et al. 2007). Simulation experiments of dugong and turtle feeding in mixed species tropical Queensland meadows found changes in biomass, productivity, and species composition with recovery taking months to years depending on the grazing intensity (Aragones and Marsh 2000). A combination of natural exclusion experiments and grazing simulations in tropical seagrass meadows of the Indian Ocean with large green turtle populations have also shown a shift from climax species (*Thalassia hemprichii*) to faster growing more opportunistic species (*Cymodocea rotundata*) with increased grazing pressure (Kelkar et al. 2013). In temperate areas waterfowl are the dominant megaherbivores in seagrass systems. Grazing by black swans in New Zealand created circular feeding scars where over 90% of roots and rhizomes of *Zostera muelleri* were removed and which at high grazing intensity amounted to the annual removal of 20% of total meadow biomass (Dos Santos et al. 2012). Experiments simulating these grazing impacts found that at biomass at these high intensities biomass can take years to recovery to pre-grazed levels (Dos Santos et al. 2013). When high grazing intensity of swans was combined with other stressors that reduce light availability the rate of seagrass recovery was further reduced (Eklof et al. 2009).

### *17.7.2 Bioturbation*

Bioturbation is another faunal process that can affect the structure of seagrass landscapes. Bioturbation is the biological disturbance of particulate matter within the sediment column resulting from burrowing, or excavating by animals (Meysman et al. 2006). The impact of bioturbation on seagrass ecosystems are generally considered to be primarily negative and driven by processes such as burial, erosion, shading, destabilisation of sediments and damage to roots and rhizomes. Positive responses of seagrasses may also be stimulated by the oxygenation of sediment and removal of toxic substances such as pore-water hydrogen sulphide, and the accumulation and remineralisation of organic matter (DeWitt 2009). A growing body of research is investigating the relationship between bioturbation from a suite of fauna and seagrasses, however the number of these studies in Australia is very low.

Burrowing invertebrates such as shrimp, crabs, urchins and polychaete worms form the major focus of studies of bioturbation in seagrass meadows. Callianassid and alpheid shrimp can exist in high densities in tropical seagrass meadows and burrow to great depths, displacing large amounts of sand that form sand mounds and can bury surrounding seagrass (Kneer et al. 2013; Nacorda 2008; Suchanek 1983). These shrimp also occur in large numbers in Australian seagrass meadows (see Fig. 17.11a). Burrowing crabs such as the fiddler crabs in New Zealand *Zostera muelleri* beds (Woods and Schiel 1997) and excavation by invasive European green crabs (*Carcinus maenas*) in *Zostera marina* beds in Canada (Garbary et al. 2014) have been linked with severe declines in seagrass cover through damage to rhizomes and erosion at the edge of beds. Fiddler crabs can be found in high abundances in intertidal Australian seagrass beds and the European green crab has also been introduced into Australian estuaries (Garside et al. 2014).

Excavation for foraging by large fauna such as stingrays, turtles and dugong has also been linked to seagrass declines. Stingrays in mixed *Zostera marina* and *Halodule wrightii* in North Carolina create pits within seagrass meadows at a frequency that influence seagrass landscape patterns by disrupting bed margins and potentially affecting seedling recruitment (Townsend and Fonseca 1998). Similar pits have been observed in seagrass meadows in north-eastern Queensland (Inglis 2000). Green sea turtles which are abundant in tropical seagrass meadows of

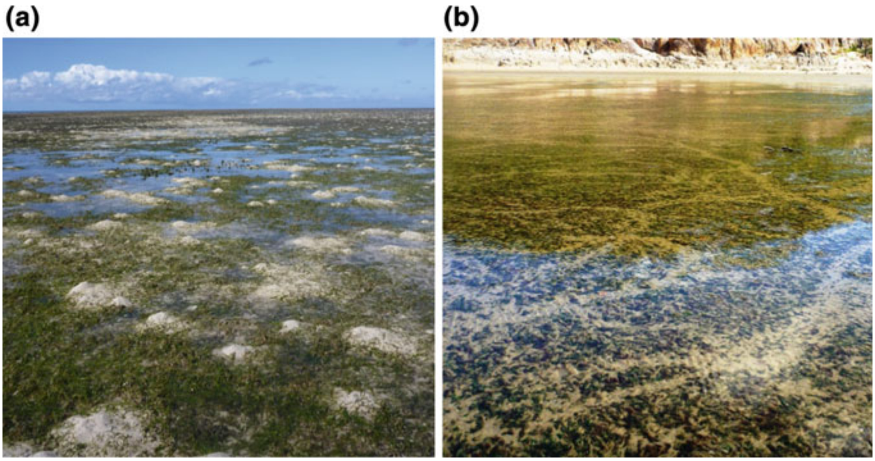

**Fig. 17.11** Bioturbation in seagrass beds caused by **a** burrow shrimp at Green Island QLD (photo by Rob Coles) and **b** excavation foraging by dugong leaving feeding trails at Cape Pallarenda QLD (photo by Samantha Tol)

northern Australia have been observed burrowing to expose rhizomes and roots for consumption when above-ground forage material is scarce (Christianen et al. 2014). This behaviour creates gaps in seagrass meadows and enhances erosion resulting in adverse effects on seagrass cover and biomass. Dugong are also known to use excavation tactics at times to access more nutritious below-ground rhizomes (Wirsing et al. 2007). This behaviour leaves behind scars in seagrass meadows known as feeding trails (Fig. 17.11b) and can lead to changes in seagrass meadow structure (Preen 1995).

## 17.8 Conclusion

Seagrass research both globally and in Australia has progressed steadily over the last few decades with substantial increases in the understanding of fauna assemblages in these habitats and the processes that regulate and drive changes in their structure. Of course there are still large knowledge gaps that require future research effort. Much more research effort has been devoted to studying temperate regions while processes in tropical seagrass meadows are comparatively poorly understood. Likewise, there is a far greater comprehension of intertidal and shallow subtidal habitats compared to deep water meadows. At fine spatial scales, the identity and ecosystem function of small invertebrate assemblages remain poorly studied and require greater focus. A recent workshop of Australian seagrass experts identified similar knowledge gaps in seagrass faunal assemblages as have been highlighted in this chapter (York et al. 2017). These include questions regarding: seascape processes such as the nursery role of seagrass habitat, trophic relay and detrital subsidy; the role of herbivory in structuring seagrass habitat, particularly in the tropics and; how do anthropogenic disturbances impact and drive changes in seagrass faunal assemblages?

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# Chapter 18
# The Roles of Seagrasses in Structuring Associated Fish Assemblages and Fisheries

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**Abstract** Seagrasses are known to provide important habitats for a diversity of fish and fisheries species. Continued research has allowed us to re-evaluate the generalisations, and identify the gaps in our knowledge regarding these habitats, particularly in an Australian context. Seagrasses generally form part of a mosaic with other habitats within a seascape that contributes to its overall biodiversity of fish. Patterns of abundance and diversity of fish between seagrass and other habitats, such as unvegetated flats and reef habitats, is inconsistent and depends on the region, fish and seagrass species, and sampling method. Edge effects, adjacent habitats, and fragmentation can strongly influence fish assemblages. Seagrass structural complexity can enhance survival and growth of juvenile fishes, but recent studies show that survival rates of individual prey do not vary greatly across seagrass densities when densities of both prey and predators increase with seagrass density. The concept of the nursery habitat has been built on data from studies in estuaries or highly seasonal seagrass habitats, whereas recent studies in marine systems or cool temperate seagrass meadows suggest that this role does not always hold. Direct grazing on seagrasses by fishes occurs mainly in tropical regions,

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although there is a paucity of data on this process along with several other processes, from tropical Australia. Grazing on seagrasses by fishes appears to be limited in temperate regions, with consumption of seagrass restricted mainly to omnivorous species. However, tropicalisation, that is, the immigration of tropical grazers to higher latitudes due to global ocean warming, is predicted to increase grazing rates on temperate seagrasses. Reductions in seagrass biomass caused by increased grazing will disrupt connectivity processes between seagrass meadows and surrounding habitats, and are likely to have significant ramifications for the biodiversity and ecosystem services those other coastal habitats provide. Although other habitats rely on inputs of seagrass detritus, and the immigration of fish and fisheries species from their juvenile seagrass habitats, quantitative data on this link are limited. Evidence that fisheries declines, either directly or indirectly, have resulted from seagrass loss is equivocal to date, and therefore, the quantification of this role is still needed. Managing seagrass for fisheries is complex, and many fisheries agencies embrace ecosystem-based management, but do not have direct responsibility for seagrass habitat. Significant progress has been made in our knowledge of fish and fisheries in seagrasses, but our review highlights significant knowledge gaps where further research is recommended.

## 18.1 Introduction

Seagrass meadows provide important habitats for a wide range of fish species. The often higher densities and diversity of fish in seagrass meadows compared to other coastal habitats, particularly sand and mud flats, reflects elevated structural complexity, primary and secondary production, and availability of vegetal detritus (Nagelkerken 2009 and references therein; Nanjo et al. 2014). These characteristics, in turn, are likely to provide increased protection from predation and food availability for both adult and juvenile fish compared to less complex habitats (Horinouchi 2007). For these reasons, seagrass meadows are perceived as important "nursery habitats" for fisheries production, and have received considerable attention, leading to several reviews over the last few decades (see Bell and Pollard 1989; Connolly et al. 1999a, b; Gillanders 2006; Heck and Orth 1980; Heck and Valentine 2006; Ogden 1980; Jackson et al. 2001; Whitfield and Pattrick 2015; Ogden 1977).

Many of the early generalisations of seagrass ecology emerged from studies carried out in the 1970s and 1980s, which led to an increasing effort in seagrass research in the 1990s and 2000s. In a search on ISI Web of Science using the keywords "fish*" and "seagrass*", a total of 2,114 papers referred to fish and seagrass between 1992 and 2015. A confirmation process for those papers revealed that a total of 601 papers (not including review papers) specifically examined at least one aspect of fish ecology in seagrass meadows. The number of papers increased from 59 in 1992–95 to 166 in 2004–07, before declining to 84 in 2012–2015 (Fig. 18.1). The majority of papers originated from Australia and North

America in the 1990s, but subsequently, studies from the Caribbean and Europe in the 2000s contributed to the literature (Fig. 18.1). There was also an increase in the number of papers coming from Africa and Asia during the 2000s. Perhaps reflecting the focus of research in narrow geographic ranges, a large number of studies has examined fish assemblages in meadows dominated by *Zostera* and *Thalassia* (200 and 137, respectively) (Fig. 18.1b). Fish in *Posidonia* and *Halodule* meadows received less attention (74 and 66 papers, respectively) (Fig. 18.1b). However, *Posidonia* received far greater attention in the 2000s, mainly associated with increased work in the Mediterranean Sea. Fish assemblages in other seagrasses, including *Amphibolis*, *Cymodocea*, *Enhalus*, *Halophila*, *Syringodium* and *Thalassodendron,* have received little attention.

In this chapter, we examine the importance of seagrass meadows to fish and fisheries, either directly as a habitat and food source, or indirectly through the

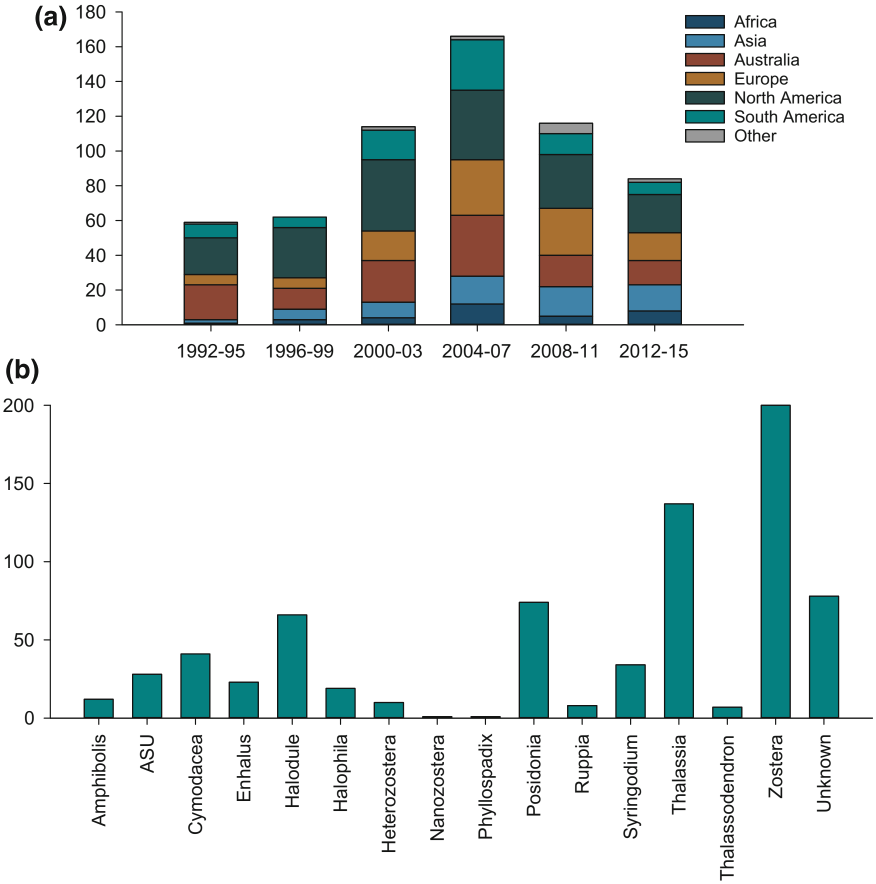

**Fig. 18.1** The number of primary publications examining fish in seagrass meadows in **a** different years and regions, and **b** different seagrass genera

provision of seagrass-associated organic matter to other habitats. We generally focus on finfish, but broaden the scope to include invertebrates when discussing fisheries. A recent increase in the number of published studies examining fish in seagrasses in a range of seagrass genera and regions around the world (Fig. 18.1), allows us to examine whether early generalizations regarding the use of seagrass meadows by fish hold for a broad suite of seagrass genera and geographic regions, and discuss these in the context of Australian seagrasses where possible. We firstly consider the spatial and seascape patterns in diversity of fishes by examining fish assemblages in seagrass meadows compared to other habitats, including comparisons across different seagrass habitats and depths, and exploring the current knowledge of structure, patch size and edge effects. We then focus on assessing the generalisations regarding the nursery function of seagrass meadows to fish and feeding ecology within those systems. We next examine the mechanisms of connectivity between seagrass meadows and coastal and offshore fisheries, focusing particularly on Australian fisheries. Finally, we discuss management issues related to seagrass and the sustainability of fisheries, followed by the main research gaps the literature that we consider need attention.

### *18.1.1 Characteristics of Seagrass Habitats*

The physical characteristics of seagrasses differ markedly among genera. In a classification proposed by Walker et al. (1999), *Zostera* and *Halodule* have low biomass, are characterized by rapid turnover, and are ephemeral (Fig. 18.2). In comparison, *Thalassia, Enhalus* and *Posidonia* have relatively high biomass, slow turnover of biomass, and are persistent (Fig. 18.2, Hemminga and Duarte 2000). The different growth forms respond differently to disturbance, and are likely to interact differently with higher trophic levels (Walker et al. 1999). Furthermore, different genera have different distribution ranges, with *Zostera* exhibiting the greatest latitudinal range from the tropics to cold temperate regions (Moore and Short 2006), while *Thalassia* is restricted mainly to the tropics (Van Tussenbroek et al. 2007) and *Posidonia* to temperate regions of Australia and the Mediterranean Sea (Green and Short 2003). Also, the different forms of seagrasses occur in different coastal environments, and therefore form different associations with neighbouring coastal habitats. For example, *Thalassia* is often associated with mangroves and coral reefs (van Tussenbroek et al. 2007), while *Zostera* is often found in estuaries and *Posidonia* in marine waters (Guidetti et al. 2002; Gobert et al. 2006).

The differences in form and environment affect the interactions of seagrasses with the associated epiphytes and invertebrate fauna, and the combination of all these attributes will affect the associated fish assemblages. Seagrass species with relatively slow turnover such as *Posidonia* spp., and those with extensive and persistent stems such as *Amphibolis* spp., have high levels of epiphytic algae and sessile epifauna (Borowitzka et al. 1990; Jernakoff and Nielsen 1998). These attributes would increase food availability and habitat structure beyond the seagrass

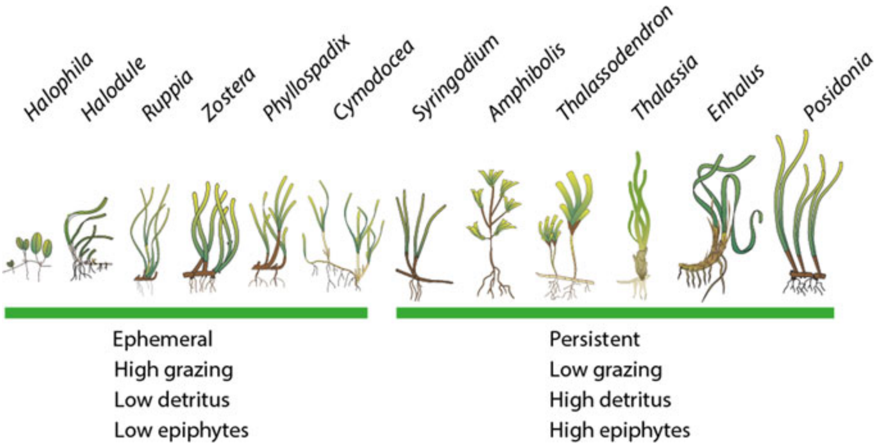

**Fig. 18.2** Conceptual model displaying the life history and functional characteristics of seagrass genera that are relevant for their roles as fish habitats (adapted from Walker et al. 1999)

itself, and influence the densities and diversity of fish assemblages in seagrass meadows. In addition, Heck and Orth (1980) suggested that there is a latitudinal shift in habitat complexity and heterogeneity, with temperate seagrass meadows being the most homogeneous and tropical meadows being the most heterogeneous through the occurrence of associated organisms such as sponges, bryozoans, corals, rhodophytes, and calcareous algae such as *Halimeda* spp. The addition of these other habitats could lead to increased diversity of fishes in seagrass meadows (Nagelkerken et al. 2015).

## 18.2 Spatial and Seascape Patterns in Diversity

In early studies, the value of seagrass as a fish habitat was often based on comparisons between seagrass meadows and adjacent unvegetated sediments. The greater diversity and densities of fish, particularly juveniles, in seagrass meadows led to the general acceptance that seagrasses provide critical nursery habitats for fish, and this was often attributed to their greater structural complexity that enhances growth and survival of juvenile fish. More recently, fish assemblages of seagrass meadows have been examined in a broader spatial and seascape context, comparing them to other structured habitats or among meadows comprising different seagrass species or different spatial configurations representing fragmentation. Also, a greater focus has been placed on the influence of connectivity between seagrass meadows and other habitats at the seascape scale through the movement of fish and organic matter between habitats. Below, we discuss the role of spatial and seascape factors in influencing the value of seagrass meadows as fish habitats.

### *18.2.1 Seagrass Versus Unvegetated Sediments*

Species richness and densities of fish are most often higher in seagrass meadows than unvegetated sediment throughout the world, including Australia (Ferrell and Bell 1991; Franco et al. 2006; Connolly 1994b), but there are exceptions (Heck and Thoman 1984). While those general conclusions have often been based on meadows comprising smaller species, such as *Zostera* spp, they have also been observed for meadows of larger seagrasses, such as *Posidonia* or *Amphibolis.* In expansive studies across southern Australia, Edgar and Shaw (1993, 1995) showed that fish production was usually, but not always, greater in shallow seagrass meadows comprising either *Posidonia* or *Zostera* than adjacent unvegetated sediment. At some locations, fish production and abundances were far higher over sand than in *Posidonia* meadows (Edgar and Shaw 1993, 1995), while other studies have shown similar abundances between *Posidonia* or *Zostera* meadows and adjacent sandy areas (Hyndes et al. 2003; Gray et al. 2011). Furthermore, abundances of fish are not always greater in seagrass compared to sandy areas in *Thalassia* meadows of the Caribbean Sea/Central America region (Adams and Ebersole 2004; Arrivillaga and Baltz 1999; Sheridan et al. 1997) and *Enhalus* meadows in Japan (Nakamura and Sano 2004). These inconsistent patterns likely relate to the landscape structure or density of the seagrasses (Hyndes et al. 2003), or other factors such as sampling bias and diel differences in fish assemblages.

Many studies have compared fish assemblages across habitats during the day, but fish assemblages can shift between day and night (Harmelin-Vivien 1982; Gray et al. 1998; Johnson et al. 2008). Such diel shifts can reflect the movement of certain species in and out of seagrass during the diel cycle. For example, a comparison of fish in Australian *Posidonia* meadows and adjacent bare sediment by Hyndes (unpublished data) showed far higher densities of fish in the former habitat during the day, but no differences at night. However, these results reflected the pronounced diel differences in densities of schooling species within the family Atherinidae, whose members appear to move into shallow sandy areas adjacent to seagrass at night (Humphries and Potter 1992). This has also been observed for labrid and sparid species in *P. oceanica* meadows in the Mediterranean Sea (Guidetti 2000). However, such conclusions need to consider the ability of some species to avoid capture during the day, as highlighted by Gray et al. (1998) for the schooling *Liza argentea*. From the above, any assessment of seagrass meadows as fish habitat against unvegetated sediments needs to consider location of the habitat, species of seagrass, and potential sampling biases (e.g. time of day and type of sampling gear).

### *18.2.2 Differences Among Seagrass Species*

Coastal environments can contain a mosaic of seagrass meadows comprising a number of species, and it is overly simplistic to assume that all seagrass meadows provide the same functions. While there has been considerable attention paid to the role of meadow structure, few studies have compared fish assemblages across different seagrass habitats that vary markedly in their species composition and physical structure (Fig. 18.2). For example, species diversity and densities of fishes differ substantially between meadows of *Enhalus acroides* and *Thalassia testudinum* in Zanzibar (Gullström et al. 2008) and *Halodule wrightii*, *Thalassia hemprichii* and *Syringodium filiforme* in the Gulf of Mexico (Ray et al. 2014). In Australia, several studies have shown that fish assemblages differ between meadows of *P. australis* and *Z. capricorni* in eastern Australia (Middleton et al. 1984; Rotherham and West 2002; Young 1981), although these differences may reflect depth gradients across different seagrass species. Similarly, fish assemblages in *P. oceanica* beds differ from those in beds of the smaller *Zostera* and *Cymodocea* species (Bussotti and Guidetti 1999), which may reflect the seasonal dynamics of the seagrasses. That is, the canopy of *P. oceanica* is present year round (Guidetti et al. 2002), while that of small-sized seagrasses almost disappears in the winter (Guidetti and Bussotti 2000). Also, on the west coast of Australia, fish assemblages in *Posidonia sinuosa* and *Amphibolis griffithii* differ (Fig. 18.3, Travers and Potter 2002; Hyndes et al. 2003). Hyndes et al. (2003) suggested that the greater biomass and size of fish in *Amphibolis* meadows is related to the space among the long, permanent stems below the canopy of *Amphibolis,* along with the high load of epiphytes on those stems, allowing larger fish to occupy and forage in those gaps. The influence of seagrass structure on fish assemblages has been tested using simpler structural characteristics such as leaf density and height (see later section), but more complex measures of structural complexity as well as food availability need to be examined.

Even for seagrass species of the same genus, fish assemblages can differ substantially. This is highlighted through comparisons of Australian *Posidonia* species, in which species richness and densities can be greater in *P. sinuosa* than over sand, while such differences are not apparent for *P. coriacea* (Hyndes et al. 2003). *Posidonia coriacea* belongs to the *Posidonia ostenfeldii* group of species that form patchy clumps of seagrass in more dynamic sandy environments compared to *P. sinuosa* in the *P. australis* group that form continuous meadows in more stable environments (Gobert et al. 2006). The lack of differences between fish assemblages in *P. coriacea* and sand (Fig. 18.3) likely reflects the presence of large sand patches within this habitat. At the finer patch scale, fish assemblages are likely to differ between seagrass and sand, but the degree of such differences will depend on patch size and edge effects (see below). Thus, the landscape structure of seagrass species, even within a genus, could have a profound influence on fish assemblages occupying seagrass habitats.

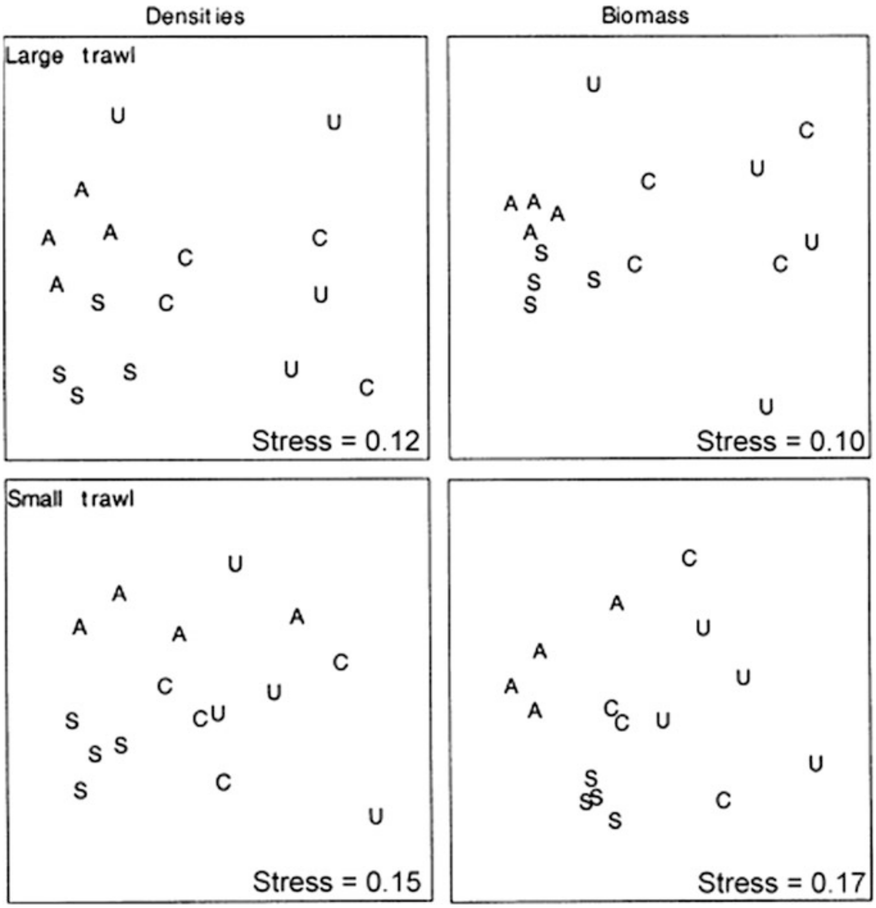

**Fig. 18.3** From Hyndes et al. (2003). nMDS ordination plots of the denisties and biomass of fish assemblages recorded in seagrass meadows comprising different seagrass species and unvegetated areas in south-western Australia using two different trawling methods. A = *Amphibolis griffithii*, C = *Posidonia coriacea*, S = *Posidonia sinuosa*, U = unvegetated areas

The different forms of seagrasses and their meadows, and their associated organisms, such as macroalgae, mangroves, corals and sponges, introduce additional layers of complexity when attempting to generalise about the role of seagrass for fish communities. Clearly, the mosaic of different seagrass species in the coastal region contributes to its overall biodiversity of fish, and the threat of replacement of one seagrass species with another (Pogoreutz et al. 2012) is likely to have significant ramifications for the biodiversity and ecosystem services these coastal ecosystems provide.

### *18.2.3 Seagrass Versus Other Structured Habitats*

Much of the discussion on the value of seagrass as a habitat has focused on seagrass versus unvegetated sediment (see above), while few studies have compared fish assemblages between seagrass and other forms of structured habitats such as reefs. Jenkins and Wheatley (1998) showed that fish assemblages were more similar between structured habitats (*Zostera* and algal reef) than unvegetated sediment, while densities and species richness did not differ between the two structured habitats. In comparison, Sogard and Able (1991) showed a hierarchy in densities of fish in habitats, firstly those in *Zostera*, then the filamentous green alga *Ulva*, and then unvegetated mud. Guidetti (2000) showed that species richness was greater in *P. oceanica* than on nearby rocky reefs with macroalgal cover, while densities of fish were similar in the two habitats. While the species composition differed between the two habitats, they were more similar to each other than when compared to unvegetated sediment (Guidetti 2000). Species that make part of artisanal fishing catches, like the sparids *Diplodus annularis* and *S. cantharus* and the labrid *S. ocellatus* occurred predominantly in *P. oceanica*, while the economically and ecologically relevant sparid *D. sargus* and a range of labrids occurred mainly over rocky reef. However, *D. annularis* also settles into macroalgae of the northern Adriatic where seagrasses are not present (Guidetti and Bussotti 1997). In another study, densities of larger *S. ocellatus* were higher over rocky reef than *P. oceanica*, but medium-sized fish were more abundant in the seagrass (Mouillot et al. 1999). In comparison to those studies, Francour (1994) showed that, in Corsica, the density and biomass of fish were lower in *P. oceanica* than in rocky areas, particularly inside a marine reserve. However, outside the no-take area, densities were similar in the two habitats. Thus, there appears to be no consistent pattern among regions, but results may be strongly dependent on local fishing pressure (Minello et al. 2003; Sheridan and Hays 2003). In addition, the methods used to assess fish density or biomass could have influenced these trends. For example, large species mainly inhabit reefs at adult stages, while juveniles occupy seagrass meadows (Francour 1994; Dorenbosch et al. 2005; Campbell et al. 2011). If the sampling technique does not effectively record these large-sized species, the calculated density or biomass will be underestimated.

### *18.2.4 Influence of Depth*

Amongst seagrasses that form beds of dense and tall plants, the species with the widest depth distribution is *P. oceanica* (from the surface to 40 m; den Hartog 1970). Several species of *Halophila* occur from the surface to depths of 30 m or more (Den Hartog 1970), but the diminutive *Halophila* species modify the environment much less than *P. oceanica*, which forms a thick mat of dead and living rhizomes and roots. There have been limited comparisons between fish faunas in shallow versus deeper meadows, but a greater biomass of herbivorous fish has been observed in shallow (1–5 m) versus deep (15–20 m) *P. oceanica* meadows of the Mediterranean (Francour 1997), and juvenile sparids (*D. annularis* and *S. cantharus*), and the labrid (*Symphodus* spp.), were observed mainly in shallower waters (Francour 1997; Bussotti and Guidetti 1999; Francour and Le Direach 1994, 1998). Similarly, Travers and Potter (2002) showed greater species richness and densities of fish in shallower meadows of both *Posidonia australis* and *Amphibolis antarctica* across depths in Shark Bay on the west coast of Australia. Based on this, differences in the fish assemblages in *Posidonia australis* and *Zostera capricorni* in Australia (Middleton et al. 1984) and *P. oceanica* and a complex of *Cymodocea nodosa* and *Zostera noltii* in the Mediterranean (Guidetti 2000) could be confounded by the smaller seagrass species being located in shallower water. Middleton et al. (1984) showed that smaller species and smaller individuals of some species occupied *Z. capricorni* while larger individuals occupied *P. australis*. This could result from larvae of some species settling preferentially into *Zostera* and subsequently migrating to *Posidonia* meadows (Middleton et al. 1984) or preferentially settling into shallow habitats, regardless of structure, where predation levels may be lower (Ruiz et al. 1993) and growth rates higher (Sogard 1992).

### *18.2.5 Structural Complexity*

There is considerable longstanding evidence of a significant positive relationship between seagrass density and the abundance of small resident and transient fishes, and this type of relationship has been reported from individual seagrass meadows across the globe (see Gillanders 2006 for a review). However, this significant relationship between seagrass density and fish abundance does not always exist at larger spatial scales (that is, among, as opposed to within, seagrass meadows), and sparse meadows may sometimes harbor higher fish densities than dense meadows, a point made and discussed in some detail by Bell and Westoby (1986) in south-eastern Australia 30 years ago. The usual explanations for the large number of juvenile fishes in seagrass meadows is that they survive and grow at higher rates in structurally complex habitats like seagrass meadows, and data generally, but not always, support these explanations (Fig. 18.4, Heck et al. 2003). Bell and Westoby (1986) and Bell et al. (1987) tried to understand the reasons for such differences and proposed that stochastic settlement from the plankton could explain the inconsistencies at larger scales, with young-of-the-year fish choosing to settle in the first, but not necessarily the most dense, meadows they encountered when recruiting from offshore waters, and later redistributing themselves into preferred parts of the meadows in which they settled.

Recent studies, using different experimental procedures, help understand the variance existing between local and regional seagrass density and juvenile finfish and shellfish abundance of the type discussed by Bell and Westoby (1986). Earlier tank experiments increased only prey, not predator densities, with increasing

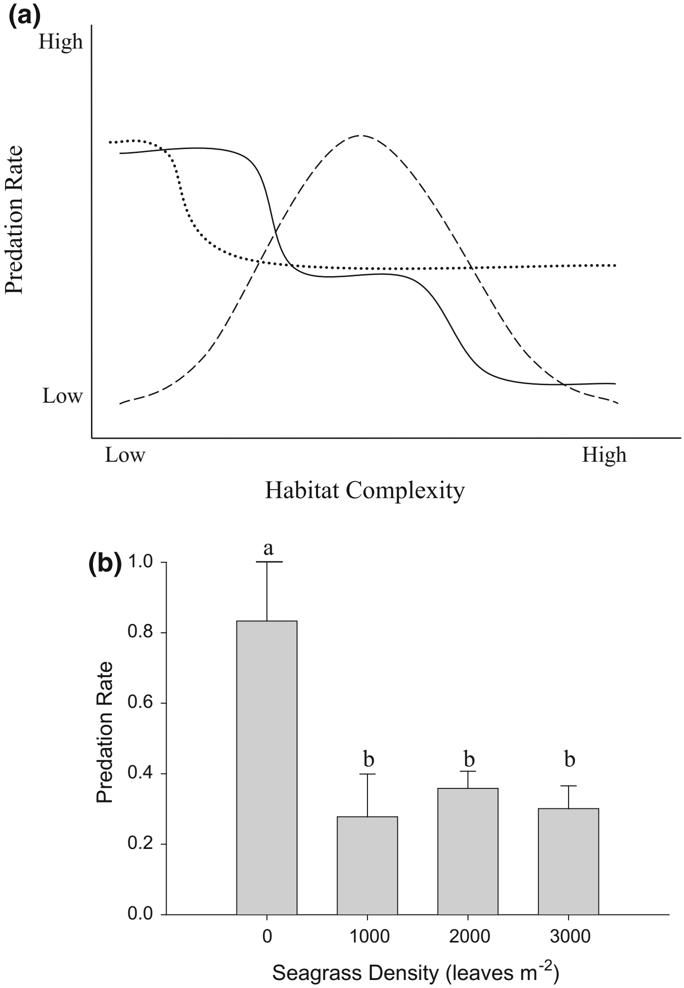

**Fig. 18.4** **a** Models describing the relationship between habitat complexity and predator success: (dotted line) Canion and Heck (2009), (solid line) Nelson (1979) and (dashed line) Crowder and Cooper (1982). **b** Predation rate (mean ± S.E.) of *Lagodon rhomboides* on *Palaemonetes pugio* in field experiments in Perdido Bay, FL by Canion and Heck (2009). Letters indicate significant differences (One-way ANOVA, $p < 0.005$)

seagrass density to examine the relationship between seagrass density and predation rate. However, recent studies of predator-prey relationships in mesocosms (e.g. Canion and Heck 2009, Mattila et al. 2008; Scheinin et al. 2012) showed that when densities of both prey and predators were increased with seagrass density (as they typically do in nature), the survival rate of individual prey was no different among a wide range of seagrass densities (Fig. 18.4). Survival in any density of seagrass was, however, clearly higher than on unvegetated substrates, thereby demonstrating the survival benefits of recruiting into seagrass habitats regardless of shoot density. Thus, it is likely that the first meadow encountered by a post-larval fish is a good choice for settlement.

### *18.2.6 Edge Effects and Fragmentation*

Seagrass meadows are often spatially heterogeneous (patchy) habitats from fine spatial scales to seascape scales, resulting from variation in a range of environmental and biological factors that affect their distribution (Bostrom et al. 2006). These heterogeneous characteristics are often expressed as seagrass patch sizes, edge characteristics and fragmentation patterns. Understanding the effect of fragmentation of seagrass meadows on fish assemblages is crucial due to the ongoing worldwide loss of seagrass (Waycott et al. 2009) and the associated fragmentation of seagrass meadows. The resulting smaller, fragmented patches of seagrass increase edge to area ratios, which can either negatively or positively affect fish depending on their preference for the interior or edge of the meadow. Fragmentation is a process, but many studies that have examined its effect on fish assemblages have used a static state as a representation of the process of fragmentation (Bostrom et al. 2006; Macreadie et al. 2009). Studies in south-eastern Australia that simulated fragmentation using artificial seagrass units (ASUs) showed that loss of seagrass area during fragmentation may not lead to reduced fish abundances if fish are more abundant at the edge of seagrass meadows (due to increased perimeter/area ratio), as occurred in this case with pipefish (Macreadie et al. 2009). Moreover, these studies showed that treatments that were actively fragmented had higher species richness than those already fragmented at the start of the study, illustrating the difference in the effects of fragmentation compared to static patchiness (Fig. 18.5) (Macreadie et al. 2009). In the Mediterranean Sea, Vega Fernandez et al. (2005) reported interesting results based on a *P. oceanica* meadow that was partially destroyed by excavation, resulting in areas of seagrass habitat of equal shoot density but different degree of fragmentation. The fish assemblages associated with differently fragmented beds showed fairly variable patterns: (i) for some species, the abundance was positively related to the degree of fragmentation, (ii) some species were more abundant in fragmented beds, without any difference related to with the degree of fragmentation, (iii) some species were more abundant in large seagrass patches or in the continuous meadow.

Earlier studies did not show strong evidence for seagrass edge effects on fish distributions (Connolly and Hindell 2006). Most studies showed no edge effect, and for those that did show an effect, fish abundances either increased (positive effect) or decreased (negative affect) near the edge. Many studies inferred edge effects from studies of different patch sizes (smaller patches have a larger perimeter/area ratios (Bell et al. 2001), but assumptions that changes in faunal abundance in differing patch sizes are due to edge effects is not well founded (Connolly and Hindell 2006). However, recent studies have made more direct measurements of the

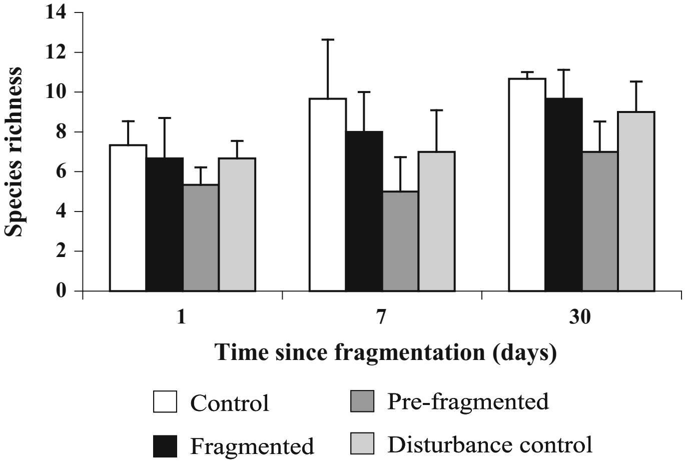

**Fig. 18.5** Modified from Macreadie et al. (2009). Mean species richness (±standard error) in artificial seagrass units. Treatments for the fragmentation experiment were constructed from artificial seagrass units (1 $m^2$) and included: Control, a continuous 9-$m^2$ patch; Fragmented, a 9-$m^2$ patch fragmented to 4 single 1-$m^2$ patches (resulting in a 56% loss of seagrass habitat); Pre-fragmented (PF), 4 single 1-$m^2$ patches; and Disturbance control, fragmented and then immediately restored to a continuous 9-$m^2$ patch

distribution of fish in seagrass meadows, or have used an experimental approach with artificial seagrass units (ASUs). Direct measurements of fish distribution in *Zostera* beds in south-eastern Australia showed strong edge effects for some species: pipefish (Syngnathidae), weedfish (Clinidae) and gobies (Gobiidae) showed positive effects, while garfish (Hemirhamphidae) and weed whiting (Labridae) showed negative effects (Smith et al. 2008, 2012). These effects were, however, not uniform in space or time. For example, pipefish were influenced by edge effects on the seaward but not landward edge of the beds, while weedfish only showed an effect at night (Smith et al. 2008). Edge effects for both these taxa varied with patch size, indicating that patch size cannot be used as a simple proxy for edge effects, and that both patch size and edge effects must be considered (Smith et al. 2010). Furthermore, edge effects may vary over the life cycle of fish. For example, King George whiting (Sillaginidae) showed a negative edge effect for small recruits (Smith et al. 2011) but a positive edge effect for older juveniles (Smith et al. 2012).

Heterogeneous characteristics of seagrass meadows, such as patch size and edge effects, can influence fish assemblages by altering: (1) water flow, physical disturbance and sediment structure; (2) predation pressure; (3) movement and behaviour of fish; and (4) reproductive strategies of fish (Bostrom et al. 2006; Macreadie et al. 2009). In support of some of these mechanisms, recent studies in south-eastern Australia showed that fish displaying edge effects were influenced by variation in the physical structure of seagrasses (Smith et al. 2008), the distribution of food resources (Macreadie et al. 2010), and the influence of predators (Smith et al. 2011).

Experiments using ASUs showed that the positive edge effect for pipefish in *Zostera* was related to food resources (Macreadie et al. 2010), in particular the supply of copepod prey in the water column for these ambush predators (Macreadie et al. 2010; Warry et al. 2009). In contrast, negative edge effects for King George whiting recruits are likely the result of predation effects, with tethering studies showing that predation by piscivorous fish was much higher near the edge of the bed than its interior (Smith et al. 2011). In summary, recent mensurative and manipulative experiments in temperate Australia show that many fish species exhibit strong, but variable, responses to seagrass edges and fragmentation.

## 18.3 Role of Seagrass as a Habitat

The functional roles of seagrasses as habitat varies among species, which use seagrass beds as permanent and seasonal residents, transients and occasional migrants (Kikuchi 1974). Much research has focused on seasonal residents, particularly those recruiting into meadows as larvae or juveniles before migrating to other habitats, which has led to seagrasses being considered critical “nursery” habitats for many economically important species.

### *18.3.1 Nursery Role*

For decades, seagrass meadows have been considered to provide critical nursery habitats, principally due to many earlier studies demonstrating high abundances of juveniles in seagrass meadows compared to unvegetated substrates (see Beck et al. 2001), and the large number of economically important species using seagrass meadows as juveniles. The underlying premise of the nursery role is that juveniles in a putative nursery habitat should disproportionately contribute to the adults in other habitats, through some combination of greater densities, growth rates and survival of juveniles in the nursery habitat, followed by their successful movement to adult habitats (Fig. 18.6, Beck et al. 2001). In support of the nursery role of seagrass meadows, a meta-analysis by Heck et al. (2003) showed that density, survival and growth of fish were generally greater in seagrass meadows, although this generality did not hold as well between seagrass and unvegetated areas in the Southern Hemisphere, or between seagrass and other structured habitats, such as saltmarshes (Heck et al. 2003). Heck et al. (2003) showed that growth rates of fish are generally greater than in surrounding unvegetated areas, but not necessarily other structured habitats. This suggests that structure and presumably increased food availability associated with habitat structure, play major roles in supporting increased growth rates. Similarly, structurally complex habitats increase survival by reducing the foraging success of predators (Heck et al. 2003). Nevertheless, there is still limited evidence that seagrass meadows disproportionately support juveniles

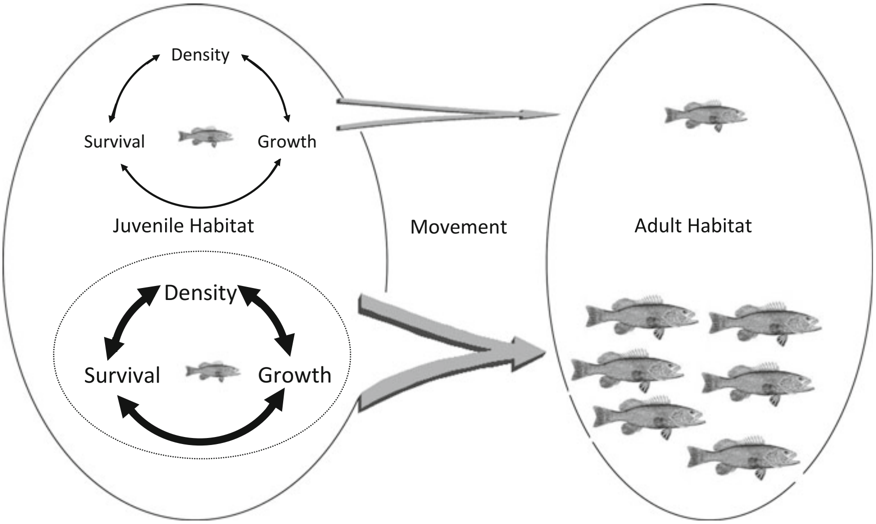

**Fig. 18.6** Conceptual diagram of the nursery role concept (adapted from Beck et al. 2001). Size of symbols represents the relative magnitude

that contribute to the adult stages of fish populations, due to the difficulty of assessing the movement patterns of juveniles from seagrass meadows into adult habitats. A recent, update meta-analysis by McDevitt et al. (2016) confirmed most of the generalisations reported by Heck et al. (2003), thereby strengthening the support for the seagrass nursery hypothesis.

Dahlgren et al. (2006) have further developed the discourse around the nursery role hypothesis by proposing the new term “Effective Juvenile Habitat” or “EJH”, in which an EJH should contribute more juveniles on average to adult habitats than the average of all juvenile habitats. However, this can only be evaluated by determining the proportion of fish in adult habitats that originate from all possible juvenile habitats. Recent advances in microtagging, otolith microchemistry and stable isotopes are allowing this to be tested (e.g. Gillanders and Kingsford 1996), but progress has been slow due to the complexity and cost of such studies.

Extensive meadows of many seagrass species are restricted to the protected waters of estuaries (see Green and Short 2003), which can be extensively used as juvenile habitats (Sogard 1992), regardless of whether seagrass is present. The concept of the nursery habitat was built around the focus of many studies on estuaries (Beck et al. 2001), leading to a bias towards estuarine systems (e.g. Chesapeake Bay, Jones 2014). Indeed, the meta-analysis by Heck et al. (2003) indicated that warm temperate and tropical seagrasses in the Northern Hemisphere appeared to play a more important nursery role than those in cool temperate and boreal waters (Heck et al. 1989; Heck and Coen 1995). In Australia, seagrass meadows are extensive in sheltered estuarine and marine waters as well as more exposed and open marine waters (Abrantes et al. 2015). In this context, in expansive studies across southern Australia, Edgar and Shaw (1993) and Edgar and Shaw (1995) demonstrated the highly variable use of seagrass as a juvenile habitat for fish. Edgar and Shaw (1995) considered the lower abundances of juvenile fish in seagrass meadows along southern, as compared to eastern Australia, to be related to the focus of studies on estuarine versus marine environments in the respective regions. This was supported by studies of more exposed waters along the west coast of Australia, where seagrasses played a minimal role as a juvenile habitat (Travers and Potter 2002; Hyndes et al. 2003).

Although not mutually exclusive, the dynamics of seagrass as a habitat provides another explanation of the observed variation in the role of seagrasses as juvenile habitats. Many species of seagrass are highly seasonal in above-ground biomass, e.g. *Halodule*, *Zostera* and *Thalassia* (Hemminga and Duarte 2000). The highly ephemeral nature of these seagrasses means that habitat availability is not consistent throughout the year, and therefore, it is perhaps not surprising that fish do not use these habitats throughout their life cycles. For example, the seasonal variability in leaf density of *Cymodocea nodosa* and *Zostera noltii* compared to *P. oceanica* in the Mediterranean Sea appears to result in different fish assemblages in those habitats (Guidetti 2000). However, persistent (or perennial) species such as those of *Posidonia* provide above-ground biomass throughout the year, allowing fish species to occupy these productive habitats throughout their lifecycles, and therefore resulting in a smaller proportion of fish utilizing seagrasses as juvenile habitats alone (see section below). In southern Australia, the seagrasses *Posidonia australis*, *P. sinuosa* and *Amphibolis antarctica* and *A. griffithii* form extensive meadows, and studies in these meadows have formed the majority of those concerning seagrass-associated fish in the region (Travers and Potter 2002; Hyndes et al. 2003; Edgar and Shaw 1993, 1995). The perennial nature of these seagrasses would allow resident species to occupy structured habitats throughout their life cycles, and these species characterize those meadows in southern Australia (see below). Conversely, the ephemeral nature of other seagrass species would prevent species that require structure to remain in those habitats when the above-ground biomass is absent in the winter months. Supporting this hypothesis, meadows of *Zostera capricorni* in estuaries on Australia's east coast provide a juvenile habitat for a range of species (Smith and Sinerchiab 2004). The seasonality of seagrass meadows would alter the availability of this habitat through the year, which would have presumably had a profound effect on the evolution of life history strategies of fish in coastal waters.

The economically important *Sillaginodes punctatus* provides a useful cautionary example of generalizations regarding the role of seagrasses as a nursery habitat. Young-of-the-year of this species recruit into *Zostera* meadows in south-eastern Australia (Robertson 1977; Connolly 1994a, c; Jenkins et al. 1997; 1998), but can also recruit to reef algae (Jenkins and Wheatley 1998) and sandy areas in some locations (Jenkins and Hamer 2001). In comparison, the species appears to recruit only into sheltered sandy areas rather than *Posidonia australis* meadows in south-western Australia (Hyndes et al. 1997; 1998). The presence of seagrass, therefore, does not appear to be the primary requirement for successful recruitment of this species. Indeed, the higher recruitment of *S. punctatus* into more sheltered unvegetated habitats where food availability is higher (Jenkins and Hamer 2001), suggests that food availability drives habitat choice of the recruiting juveniles of this species. In support of this conclusion, experiments by Connolly (1994b, c) showed that juvenile abundances were not affected by the removal of *Zostera,* and the species' choice for *Zostera* as a habitat was over-ridden by food availability. However, higher predation on juvenile *S. punctatus* in unvegetated areas (Hindell et al. 2002), suggests that there is a trade-off between high food availability and predation in the sheltered unvegetated habitats. In addition, proximity of seagrass meadows to the currents and wind conditions that transport larvae into coastal habitats appears to play a major role in the recruitment of this species (Jenkins et al. 2000) and others (Ford et al. 2010) into juvenile habitats in the region.

### *18.3.2 Seagrass for Residents*

The ability of fish species to complete their life cycles in seagrasses would require the persistence of the habitat in suitable conditions for reproduction to occur. Firstly, as stated above, many studies on seagrass-associated fish have been carried out in estuaries, which are used for extensive periods by the juveniles of many species before returning to the marine environment to spawn (Potter et al. 2015). While not mutually exclusive, the presence of above-ground biomass of particularly persistent species of seagrasses, such as *Posidonia* spp. in coastal marine waters of southern Australia and the Mediterranean Sea, is likely to provide habitat for juveniles and adults of many seagrass-associated species throughout the year (Bell and Harmelin-Vivien 1982; Edgar and Shaw 1993; Harmelin-Viven 1984; Hyndes et al. 2003). Resident species, therefore, appear to be common in meadows in coastal marine waters, but the proportion of life-long residents may also be related to depth, since *P. oceanica* meadows in shallow (3 m depth) waters of the Mediterranean Sea contain more juveniles (Francour 1997; Guidetti and Bussotti 1997; 1998) than those in relatively deep (12–18 m) waters (Bell and Harmelin-Vivien 1982; Harmelin-Viven 1984).

Fish assemblages in persistent, marine seagrass meadows are likely to be influenced by the reproductive and early life history strategies of resident species. For example, several resident fish families common to *Posidonia* meadows, e.g. Syngnathidae, Apogonidae and Monacanthidae (Kendrick and Hyndes 2003; Steffe et al. 1989) and Labridae (Bell and Harmelin-Vivien 1982; Francour 1997) are characterized by parental care such as mouth brooding, giving birth to live young, or depositing demersal eggs in nests (Patzer 2008). The larvae from species with these reproductive strategies may therefore recruit directly and earlier into the natal or nearby seagrass meadows of their parents, and bypass the high potential for mortality in the pelagic phase and other recruitment processes and potential bottlenecks that influence the settlement of pelagic larvae into seagrass meadows.

## 18.4 Feeding Ecology of Fish Assemblages

A range of feeding guilds occurs in the fish assemblages in seagrass meadows worldwide: (1) predators of fish and other larger nekton; (2) meso-carnivores feeding mainly on small crustaceans, such as copepods and amphipods, shrimps or molluscs; (3) omnivores that feed on mobile or sessile epifauna, as well as epiphytic algae and/or seagrass; (4) herbivores that feed on epiphytic algae and/or seagrass; and (5) detritivores that consume detritus within the meadow. Fish assemblages in southern Australian seagrass meadows are dominated by meso-carnivores feeding mainly on small crustaceans or molluscs (Edgar and Shaw 1993, 1995; Connolly et al. 2004), which in turn, often feed on epiphytes and detritus (Cook et al. 2011; Ebrahim et al. 2014). These meso-grazers play critical roles in controlling epiphytic algae on seagrass leaves in Australia (Cook et al. 2011; Ebrahim et al. 2014) and elsewhere (Myers and Heck 2013; Whalen et al. 2013), and contribute to secondary production (Lepoint et al. 2000; Smit et al. 2005, 2006; Vizzini and Mazzola 2003; Vizzini et al. 2002).

Evidence for direct grazing on seagrasses comes mainly from tropical systems (Valentine and Duffy 2006). However, it must be recognized that the trophic structure we see in seagrasses today may not reflect those of the past due to the direct and indirect effects of historical over-harvesting of large predators and grazers (Jackson et al. 2001). Apart from supporting dugongs, manatees and green turtles, tropical seagrass meadows can support a diversity of herbivorous fish, with species typically belonging to the families Labridae (Sparisoma clade), Acanthuridea and Siganidae (see Valentine and Duffy 2006 and references therein). Species within these families often move from coral reefs to adjacent seagrass meadows, where they can create "haloes" of unvegetated areas due to high levels of grazing (Randall 1965; Ogden 1977). Indeed, *Sparisoma radians* has been shown to consume nearly all daily seagrass production in some locations in the Gulf of Mexico (Kirsch et al. 2002). However, species richness and abundance of herbivores decrease with increasing latitude and decreasing water temperature (Floeter et al. 2005, González-Bergonzoni et al. 2012). While the processes leading to this pattern are not well understood (Clements et al. 2009), grazing on temperate seagrasses by fish is considered to be limited.

*Sarpa salpa* (Sparidae) in the Mediterranean Sea is an exception to the above generalisation. Early studies suggested a mixed diet for this species, comprising seagrass, epiphytes and reef algae (Havelange et al. 1997; Lepoint et al. 2000), with an ontogenetic shift towards seagrass (Verlaque 1990). Early studies also suggested that *S. salpa* consumed 4–15% of daily production of *P. oceanica* (Havelange et al. 1997; Velimirov 1984), but more recently, Tomas et al. (2005) found that consumption rates can exceed local production rates of temperate seagrass meadows. In some locations, seagrass biomass was reduced by as much as 50%, while epiphytic load was reduced by about 30% (Tomas et al. 2005). As a consequence, Valls et al. (2012) regarded this species as a keystone modifier (sensu Mills et al. 1993) in *P. oceanica* meadows.

Direct grazing by fishes on temperate Australian seagrasses appears to be very limited. Some consumption of seagrass has been observed in species of Labridae (from the Odacine clade), Hemirhamphidae, Monacanthidae, Tetraodontidae and Terapontidae, but these species are omnivorous, feeding predominantly on epiphytes and macro-invertebrates, and not seagrasses (Bell et al. 1978; Bell and Harmelin-Vivien 1983; Burchmore et al. 1984; Burkholder et al. 2012; Conacher et al. 1979; Macarthur and Hyndes 2007; Kwak et al. 2015). Despite evidence of some grazing on seagrasses, there is limited evidence that fish significantly influence seagrass production. Through exclusion experiments and observations, Burkholder et al. (2012) inferred that the terapontid *Pelates octolineatus* was responsible for grazing large portions of the *Halodule* and *Halophila* seagrasses in Shark Bay, Western Australia, but this species is omnivorous, feeding largely on epiphytic algae (Edgar and Shaw 1993) and therefore is likely to play a greater role in controlling epiphytes on seagrass leaves. As is true for many omnivorous species, the proportion seagrass in the diets of *Monacanthus chinensis* (Bell et al. 1978) and *Haletta semifasciata* (Macarthur and Hyndes 2007) increases with fish size. It may therefore be relevant that several omnivorous species attain relatively large sizes in perennial *Posidonia* or *Amphibolis* seagrass meadows (Hyndes et al. 2003) that form extensive meadows in southern Australia. These species are therefore likely to play a considerable role in the removal of particularly epiphytic algae in those meadows. There is limited information on grazing on seagrasses by fishes in tropical Australia, and this is clearly a research gap. Kwak et al. (2015) showed that the juveniles of a range of fish species in seagrass meadows of northern Queensland consumed very little seagrass. However, the parrotfish *Leptoscarus vaigiensis* is common in tropical Australia (Lim et al. 2016), and has been shown to consume up to 10 times the rate of local seagrass growth another Indo-Pacific region (Unsworth et al. 2007a, b). The species, therefore, has the capacity to remove considerable biomass of seagrass in the tropics. Also, with global ocean warming and the movement of tropical species to higher latitudes (Fig. 18.7), grazing on seagrasses in more temperate regions is predicted to increase (Hyndes et al. 2016).

Grazing on seagrass can vary among seagrass species. For example, *Thalassia testudium* appears to have a greater resistance to grazing than *Halodule wrightii* in Florida, USA (Armitage and Fourqurean 2006), and elevated nitrogen content can influence grazing (Goecker et al. 2005). In Western Australia, consumption rates were greater on the low-nutrient, slow-growing *Posidonia* and *Amphibolis* species compared to high nutrient, faster growing *Halodule* and *Halophila* species (Burkholder et al. 2012). Despite the low nutrient content of *Posidonia* species, approximately 80% of the organic soluble content of *P. oceanica* is assimilated during gut passage in *S. sarpa* (Velimirov 1984). This suggests that the species gains nutrients from seagrass even though seagrass fragments in its hindgut appear to be undigested. Similarly, *Monacanthus chinensis* and *Hyporhamphus melanochir* assimilate nutrients from *Posidonia* leaves (Conacher et al. 1979; Nichols et al. 1986), providing evidence that *Posidonia* supports the energetic requirements of some (albeit a small number of) fish species in both the Mediterranean Sea and Australia.

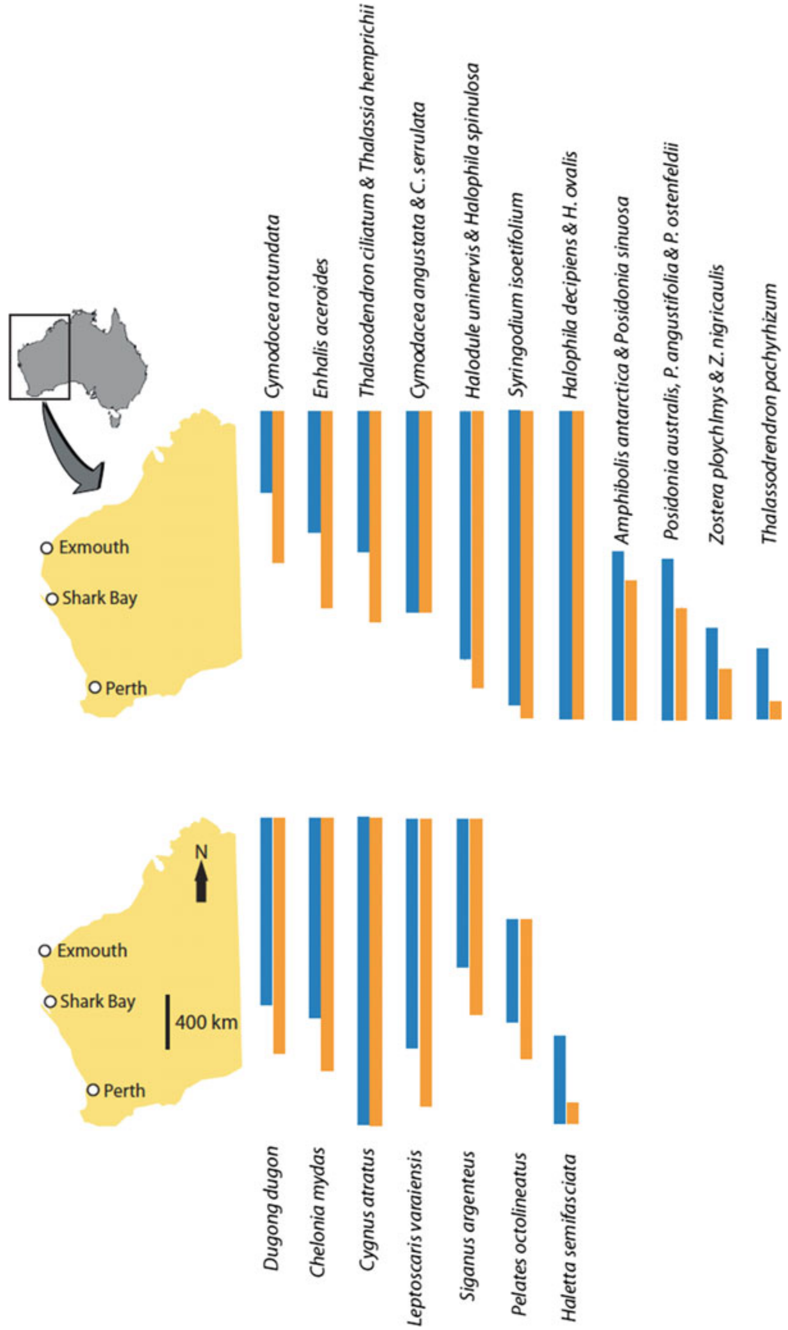

**Fig. 18.7** The current (blue) and predicted end-of-century (orange) distributions of seagrasses (top) and herbivores (bottom) along the west coast of Western Australia. See the supplemental material for methods to determine distributions and their shifts. From Hyndes et al. (2016)

## 18.5 Connectivity Across Seascapes

A major source of seascape connectivity is the process of larval dispersal from spawning in adult habitat, settlement into different juvenile habitats, and subsequent movement back to the adult habitat (Ford et al. 2010; Fowler and Short 1996; Haywood and Kenyon 2009; Verweij et al. 2008). Indeed, seascape connectivity via propagule (eggs and larvae) dispersal (at a biogeographic scale of hundreds of kms) is considered to critically affect the dynamics of fish communities associated with *P. oceanica* beds in the Adriatic Sea, in both space and time (Melià et al. 2016). The larvae of fish settling in seagrass habitats are often derived from adults in different, sometimes distant, habitats (Jenkins et al. 2000; Ford et al. 2010; Hyndes et al. 1998). This pattern of connectivity occurs in both tropical and temperate systems, with the adults of tropical species utilising coral reefs or deeper sedimentary habitats as adults (Huijbers et al. 2013, 2015; Mcmahon et al. 2012; Nagelkerken 2009; Verweij et al. 2008), and temperate species occupying coastal and offshore rocky reefs and sedimentary habitats (Ford et al. 2010, Gillanders and Kingsford 1996; Hyndes et al. 1998; Gillanders 2002; Jenkins and Wheatley 1998), and the juveniles occupying seagrass habitats in estuaries and embayments.

Use of a mosaic of juvenile habitats, termed the ‘seascape nursery’ (Nagelkerken et al. 2015), may follow a sequential pattern (Jenkins and Wheatley 1998; Pardieck et al. 1999). For example, Grol et al. (2014) showed that larvae of a coral-reef fish species initially settled into rubble habitat before moving into seagrass and then mangrove habitat with increasing size. With further growth, juvenile fish may gradually move into deeper waters before making the migration offshore (Hyndes et al. 1998). These movements from juvenile to adult habitats can occur over kilometres to 100s of kilometres (Gillanders et al. 2003; Huijbers et al. 2013; Mcmahon et al. 2012). If the adult habitat is a relatively short distance from the juvenile habitat then there may be a movement back and forth between the habitats before residence is taken up in the adult habitat (Huijbers et al. 2015). The timing of the ontogenetic migration from the seagrass nursery habitat to adult habitat may be a trade-off between higher survival in the juvenile habitat versus higher growth rates in the adult habitat (Nagelkerken 2009), or coincide with reproductive maturity and the onset of spawning (Hyndes et al. 1997, 1998).

The movement and migration of fish across a range of habitats, including seagrass meadows, significantly contributes to seascape connectivity (Olds et al. 2012; Grober-Dunsmore et al. 2008, 2009). This movement and migration may be part of the daily ambit of the individual or may have a regular diel or tidal periodicity (Krumme 2009), or may occur in the process of adults forming spawning aggregations (Nemeth 2009). Many studies have focused on fish assemblages associated with coral reefs and their proximity to seagrass habitats (Berkström et al. 2013; Olds et al. 2012; Grober-Dunsmore et al. 2009), with a general consensus that proximity of seagrass meadows to coral reefs has a significant positive effect on the assemblage structure of reef fish (Berkström et al. 2013; Olds et al. 2012). Focusing more on seagrass-associated fish, Unsworth et al. (2008) found that assemblages in seagrass were influenced by proximity to mangroves and reef, with a marked increase in fish abundance and species richness in seagrass meadows near mangroves. These links can be associated with strong diurnal and tidal migrations of fish (Krumme 2009). For example, grunts (Haemulidae) rest on patch reefs during the day but forage in surrounding seagrass meadows at night (Krumme 2009; Nagelkerken et al. 2008), while parrotfish (Scarine in Labridae) forage in seagrass during the day but hide on the reef at night (Krumme 2009). Similarly, tidal migrations of fish can connect subtidal seagrass meadows with intertidal mangrove habitats (Jelbart et al. 2007), subtidal habitats with intertidal seagrass meadows (Robertson 1980), and coral reefs with seagrass meadows (Unsworth et al. 2007a, b).

The sequential movement of fish from juvenile to adult habitats likely provides an important process for transferring nutrients across seascapes, with the series of predator-prey interactions along that path, i.e. trophic relay (sensu Kneib 1997), contributing to a net flow of nutrients to other habitats in coastal or offshore waters (Hyndes et al. 2014). This is highlighted by the estimated export of 7400 t of silver perch *Bairdiella chrysoura* from *Zostera* meadows to other coastal habitats in Chesapeake Bay, USA (Sobocinski and Latour 2015). Similarly, the ontogenetic shift of the pinfish *Lagodon rhomboides* from seagrass meadows to offshore Gulf of Mexico (GOM) is estimated to contribute approximately 25% of the overall potential production in the northeastern GOM (Nelson et al. 2013). Thus, the maintenance of the connectivity of fish assemblages between seagrass and other habitats has significant implications for conservation planning, including habitat restoration, the location of marine protected areas, and the management of fisheries. Planning must include consideration of the mosaic of inter-connected habitats in an area rather than just the characteristics of individual habitats (Berkström et al. 2013; Cheminée et al. 2014; Olds et al. 2012, 2014, 2016). In Australia, few studies have directly examined this process for fish (but see Jelbart et al. 2007), although our understanding of this process has been compiled from a range of studies for some economically important finfish species, e.g. the King George whiting *S. punctatus* (Hyndes et al. 1998, Jenkins et al. 2000), and invertebrate species, e.g. the Western Rock lobster *P. cygnus* (Chittleborough and Phillips 1975; Chittleborough 1970; Macarthur et al. 2008).

## 18.6 Seagrass Links to Fisheries

### *18.6.1 Direct Links*

There is strong evidence around the world that numerous fish and invertebrate species that support important fisheries use resources available in seagrass habitats at some stage in their life cycles (Connolly et al. 1999a, b; Jackson et al. 2001; Verweij et al. 2008; Haywood and Kenyon 2009; Mizerek et al. 2011; Jones 2014;

Lilley and Unsworth 2014; Seitz et al. 2014; Jackson et al. 2015), although the relative usage seems to vary regionally, which may in part simply reflect the amount of research in a region (Jackson et al. 2001). The usage of seagrass habitat by fisheries species is particularly well documented for Australia (Mcneill et al. 1992; Haywood et al. 1995; Jenkins et al. 1997; Connolly et al. 1999a, b; Curley et al. 2013), where species have been shown to use seagrass meadows as juvenile habitats, foraging habitats, or spawning habitats. For example, seagrass meadows in Australia are used as juvenile habitat by the King George Whiting *Sillaginodes punctatus* (Jenkins et al. 1996; Robertson 1977; Connolly 1994a) and prawns (Coles et al. 1987, 1993; Loneragan et al. 1998), a foraging habitat for the juveniles and sub-adults of the Western rock lobster *P. cygnus* (Macarthur et al. 2008, 2011), a foraging habitat for the adults of the rock flathead *Platycephalus laevigatus* (Klumpp and Nichols 1983b; Jenkins et al. 1997), and a spawning habitat for the Southern Calamari *Sepioteuthis australis* (Pecl et al. 2006). Some species, such as the grass whiting *Haletta semifasciata* and the six-spine leatherjacket *Meuschenia freycineti* are associated with seagrass throughout their entire life cycles (Jenkins et al. 1997). The southern sea garfish, *Hyporhamphus melanochir*, has an unusual link to seagrass in that the species feeds on seagrass tissue (either directly or as fragments in the water column) during the day and diurnally migrating invertebrates over seagrass beds at night (Robertson and Klumpp 1983; Klumpp and Nichols 1983a). Seagrass meadows are considered to enhance the value of fisheries linked to that habitat in south-eastern Australia by ~$A32,000 $\text{ha}^{-1}$ $\text{year}^{-1}$ (Blandon and Zu Ermgassen 2014). In the gulf waters of South Australia alone, seagrass has been estimated to contribute $A114 M per year to the economy (Blandon and Zu Ermgassen 2014; Mcarthur and Boland 2006). Similarly, the seagrass meadows of Cairns Harbour were estimated in the 1990s to contribute 178 t and $A1.2 M per year to the prawn fishery in tropical Australia (Watson et al. 1993). Based on the link between seagrass and other important fisheries around Australia, its contribution to the economy of Australia will be substantially higher. For example, in Western Australia, the fishery for the western rock lobster, whose juveniles and sub-adults in the southern part of the population forage in seagrass meadows, was valued at ~$A234 M in 2013. However, the quantification of the role of seagrasses in supporting fisheries is less clear in other regions. For example, many papers state that seagrasses, including *Posidonia oceanica*, have important nursery roles for many fishes, including commercial species in the Mediterranean. However, the quantification of this role is still in its infancy (Guidetti et al. 2009) and there has been no assessment of the related economic benefits for fisheries in that region.

### *18.6.2 Indirect Links Through Trophic Relays and Outflow of Organic Matter*

Seagrass meadows can export, on average, 0.22 kg C $m^{-2}$ $year^{-1}$, mostly in the form of leaves (Heck et al. 2008; Hyndes et al. 2014). This exported detrital material can accumulate in a range of coastal and offshore habitats. For example, accumulations of seagrass and seagrass epiphyte detritus in unvegetated mudflats adjacent to seagrass meadows of subtropical Australia support the food chain to fish, including the economically important whiting, *Sillago schomburgkii* (Connolly et al. 2005). Similarly, the transfer of seagrass detritus to nearby coral reefs in the region appears to contribute to the food resources of the labrid *Pseudolabrus guentheri* (Davis et al. 2014). The export of seagrass to more distant habitats can also support fisheries species. In south-western Australia, seagrass leaves (and kelp thalli) provide an important juvenile habitat in the surf zones for a range of economically important fish species (Lenanton 1982; Crawley et al. 2006). Furthermore, prawns in offshore waters in northern Australia (Loneragan et al. 1997), and larvae of the blue grenadier *Macruonus novaezelandiae* in offshore waters of south-eastern Australia (Thresher et al. 1992), are likely to be supported by transported seagrass detritus. Thus, the export of seagrass detritus to near and distant habitats can, at least partly, support fisheries in other coastal habitats, but direct evidence of this link is still limited.

### *18.6.3 Evidence of Links Through Seagrass Loss and Fisheries Production*

A strong dependence on seagrass by fisheries should be reflected in declining catches when seagrass is lost, however, the evidence to date is largely equivocal with seagrass loss resulting in fishery declines in some regions but not others (Connolly et al. 1999a, b; Gillanders 2005). One clear example of impacts to fisheries from seagrass loss was the marine wasting disease that caused catastrophic loss of eelgrass, *Zostera marina*, in the Atlantic basin in the early 1930s and subsequent collapse of the fishery for bay scallop, *Argopecten irradians*, on the east coast of the United States (Fonseca and Uhrin 2009). In Australia, a 70% decline in eelgrass, *Zostera*, over 10 years from the early 1970s in Western Port, Victoria, resulted in catch declines of about 40% for species known to be associated with seagrass, but not for other fishery species (Macdonald 1992; Jenkins et al. 1993). King George whiting provides a good example of this link. Prior to the 1970s, catches were variable but showed an increasing trend in three bays in Victoria (Fig. 18.8). However, after the seagrass loss in Western Port, catches declined, whereas they continued to increase in the two other nearby bays (Port Phillip and Corner Inlet).

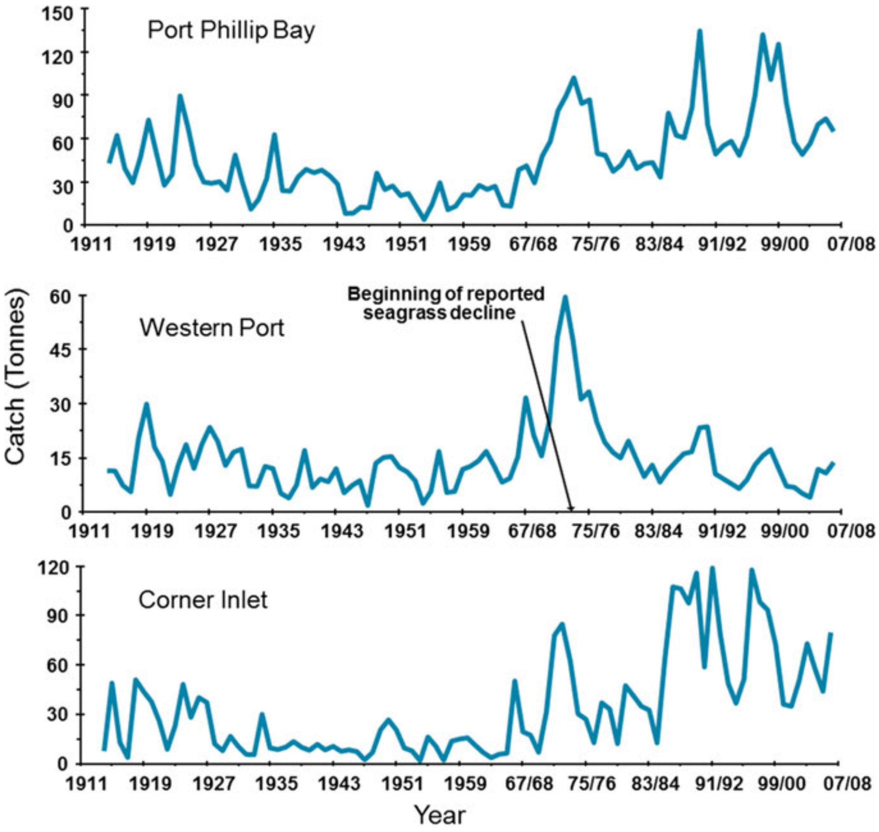

**Fig. 18.8** Historical annual catches of King George whiting from Port Phillip Bay, Western Port and Corner Inlet. Arrow indicates beginning of reported seagrass decline

In many cases, seagrass loss has not resulted in declines in fisheries linked to seagrass habitats, but this is likely to depend on the targeted species and the degree of its dependence on seagrass. For example, there was no catastrophic collapse of European fisheries associated with the eelgrass wasting disease in the early 1930s (Gillanders 2005). The equivocal link between seagrass loss and declines in fishery catches is most likely explained by facultative use of seagrass by many species, which can also use other structured habitats (Jenkins and Wheatley 1998; Heck et al. 2003). Therefore, the loss of seagrass may be ameliorated to some extent if alternative structured habitats that provide similar resources are present (Gillanders 2005; Jenkins et al. 2015). However, the level of facultative use of alternative habitats is often unknown or not quantified, making it difficult to determine the effect of seagrass loss and adaptively manage fisheries when seagrass is being lost. But if several structured habitats simultaneously decline, as is occurring in the

Mediterranean Sea for shallow *Posidonia oceanica* meadows due to coastal building (Duarte 2002) and *Cystoseira* forest due to overgrazing (Gianni et al. 2013), declines of small-scale fisheries are likely.

### *18.6.4 Management of Seagrass-Associated Fisheries*

Ecosystem-based management of fisheries is a goal now embraced by many countries including Australia (Fletcher et al. 2010; Hobday et al. 2011), and as such, includes consideration of both fishing and external impacts on seagrass (Hobday et al. 2011). Most fisheries management agencies, however, do not have direct responsibility for seagrass habitat, but rather take on an advocacy role to influence the policies of coastal and catchment managers that directly influence impacts on seagrass. Fisheries management agencies can, however, have a direct policy role in the case of fishery methods and practices that have a destructive impact on seagrass meadows (Short and Wyllie-Eciieverria 1996; Airoldi and Beck 2007) and also in the development of aquaculture areas and their associated impacts on seagrass (Delgado et al. 1997). Where seagrass is lost, fisheries managers may advocate for seagrass restoration to support and improve fisheries (Tanner et al. 2014). In the Mediterranean, the "Habitat Directive" developed by the EU provides the framework to member states to protect *Posidonia oceanica*, which is a habitat forming species of 'priority importance' for protection. Management occurs via the creation of Natura 2000 sites or other types of marine protected areas (MPAs) at national or trans-boundary levels. Also, the adoption of the Marine Strategy Framework Directive and Common Fishery Policy by EU countries drives an effort to adopt an ensemble of protection/management measures aimed at protecting the marine biodiversity and ecosystem functioning, while simultaneously supporting fisheries.

## 18.7 Gaps and Future Directions

Since the 1990s, studies on fish assemblages in seagrass meadows have expanded in terms of both the geographic range and the seagrass species forming the habitat. This has allowed us to broaden our understanding of the role of seagrass habitats to fish assemblages, but there are still a number of gaps that need addressing: (i) how seagrass loss will impact fish assemblages linked to seagrass, particularly as juveniles and their contribution to fisheries production; (ii) how habitat fragmentation versus habitat loss affects fish assemblages; (iii) how fish species interact with seagrass meadows in tropical Australia; and (iv) how temperate seagrass habitats respond to warming sea temperatures with global warming.

The 29% global areal loss of seagrass meadows since the late 1800s, and more rapid losses in the last two decades (Waycott et al. 2009), causes major concerns regarding the various ecosystem services they provide, including its importance as a habitat for fish assemblages and particularly fisheries species. Interpretation of the potential effects of seagrass loss requires a thorough understanding of the role of not only seagrass habitat in the life history of the fish, but also the potential role of alternate habitats. For many seagrass associated fish species, assumptions about the importance of seagrass habitat have been based only on sampling in seagrass habitat rather than a broader suite of potential habitats. While seagrass meadows have been estimated to enhance the value of fisheries in south-eastern Australia by $\sim$\$A32,000 ha$^{-1}$ year$^{-1}$ (Blandon and Zu Ermgassen 2014), there is limited empirical data linking seagrass-associated fish to fisheries production usually in more offshore waters, and limited data on the relative importance of different juvenile habitats in their contribution to the adult population (Beck et al. 2001; Dahlgren et al. 2006). More studies using approaches, such as otolith microchemistry and stable isotopes (e.g. (Gillanders and Kingsford 1996), are therefore needed to quantify the contribution of juveniles from seagrass meadows to adult spawning habitats for particularly fishery species. This may be more difficult to assess when fisheries in offshore regions are influenced through trophic relays of fauna originating from seagrass meadows, thereby diluting the contribution of seagrass to the offshore production. However, this export from seagrass meadows can be an important means of carbon transfer from tropical systems (Hyndes et al. 2014), and deserves attention.

While understanding fragmentation of seagrass and its effect on associated fishes is important, novel approaches are needed to separate the effects of fragmentation from seagrass loss. Seagrass loss and fragmentation tend to occur together, and therefore, the two processes tend to be confounded (Fahrig 2003). Furthermore, fragmentation is a process rather than a state, and most studies actually consider habitat configuration rather than fragmentation (Boström et al. 2006, 2011). Moreover, fragmentation effects can be further confounded by differences in within-patch structural characteristics of seagrass. Some of these issues can be addressed experimentally using ASUs (Macreadie et al. 2009), however, the scale of the experiments is inevitably small compared with seascape scales. Novel research approaches are therefore required to determine the relative importance of habitat fragmentation and habitat loss to seagrass associated fishes at seascape scales.

With less than 10% of the published studies on fishes in Australian seagrass meadows being undertaken in the tropics, there is a clear need to gain more expansive data on the role of seagrasses for fish assemblages in this climatic region. For example, our understanding of grazing by fishes on seagrasses comes mainly from tropical systems (Valentine and Duffy 2006), but predominantly from Caribbean/Gulf of Mexico region and more recently, Indonesia and Africa. Few papers (Kwak et al. 2015) have examined trophic interactions between fish and seagrasses in tropical Australia. Since species richness and abundance of herbivores is higher in lower latitudes (Floeter et al. 2005; González-Bergonzoni et al. 2012), we would expect relatively high grazing on tropical seagrasses in the region. However, this pattern needs to be confirmed, and its importance is becoming even more pronounced with global warming and the poleward shifts in the distribution of tropical species in the region.

Globally, warming waters have also increased the presence of tropical species in the harvest of finfish from temperate waters (Cheung et al. 2013), and lush kelp forests have dramatically shifted to barrens in some regions such as Australia, Mediterranean and Japan due to the poleward shift in herbivores (Verges et al. 2014). Less is known about this process known as "tropicalisation" and its impacts on temperate seagrasses. Tropical herbivores have, however, moved into seagrass meadows in temperate Gulf of Mexico, where it has been predicted that with continued immigration of those herbivores, seagrass meadows could be grazed to the "height of closely mowed lawn" (Heck et al. 2015). Hyndes et al. (2016) predicted that the influx of tropical herbivores into the temperate seagrass meadows of south-western Australia will have major consequences on the ecosystem services they provide, including a shift in food web structure from one that is detrital based to one that is mostly based on direct consumption. This would lead to reductions in the abundances of seagrass-associated fauna through reduced habitat structure and food availability (Hyndes et al. 2016). With future projections of sea temperature rises, this is clearly an issue that needs research attention in Australia and elsewhere.

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# Chapter 19
# Dugongs: Seagrass Community Specialists

**Helene Marsh, Alana Grech and Kathryn McMahon**

**Abstract** Dugongs exploit a relatively wide diet including seagrasses, macro-invertebrates and algae within intertidal and subtidal tropical and subtropical seagrass communities. The importance of seagrass genera to dugongs differs among locations and may change at the same location during times of seagrass loss. Dugongs feed by excavating or cropping, depending on seagrass morphology and the nature of the sediment. An individual dugong can disturb a considerable area of seagrass in a single day, especially in areas with low biomass. The local impact on seagrass biomass can be very significant and cause a loss of over 50% of production. The food quality of the seagrass forage eaten by dugongs is similar to the forage eaten by many wild, large, terrestrial, herbivorous mammals. Dugongs are less effective at masticating fibrous seagrasses than low-fibre seagrasses. This limitation may be most important under lengthy periods of food scarcity, such as at times of seagrass loss. The effect of dugongs feeding on seagrasses is complex and can be measured at several spatial scales including: (1) the individual feeding scar, (2) the area disturbed per day by an individual animal, and (3) the effect of a large group of animals on an individual plant community and using several responses variables: (1) microbial processes, (2) above- and below-ground plant biomass, (3) plant species composition, (4) plant nutrients, (5) invertebrate community composition and detritus, plus (6) the time taken by each of these variables to return to the pre-disturbed condition. Marked temporal fluctuations in dugong mortality and fecundity track major changes in the seagrass communities on which dugongs depend for food.

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## 19.1 Introduction

> ….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 channelled through the guts of herbivores, particularly sirenians. (Domning 2001 p. 45).

Despite this assertion, seagrass scientists increasingly acknowledge the importance of herbivory in tropical seagrass ecosystems (Valentine and Duffy 2006). The local effects of dugongs on subtropical and tropical seagrass ecosystems can be significant, especially in Australia, which not only has vast tropical and sub-tropical seagrass meadows stretching thousands of km$^2$, but also supports globally significant dugong populations. For example, Preen (1995a) estimated that a group of some 460+ dugongs consumed more than 151,000 tonnes (wet weight) of *Halophila ovali*s from 41 ha in Moreton Bay, Queensland, in under 17 days, reducing shoot density by about 95%.

This chapter explores the relationship between dugongs and their seagrass habitats in Australian waters. Australia is the dugong's stronghold (Marsh et al. 2002, 2011) and the dugong's winter range extends across the northern half of the continent from Shark Bay in the west to Moreton Bay in the east and down to Newcastle in summer (Fig. 19.1).

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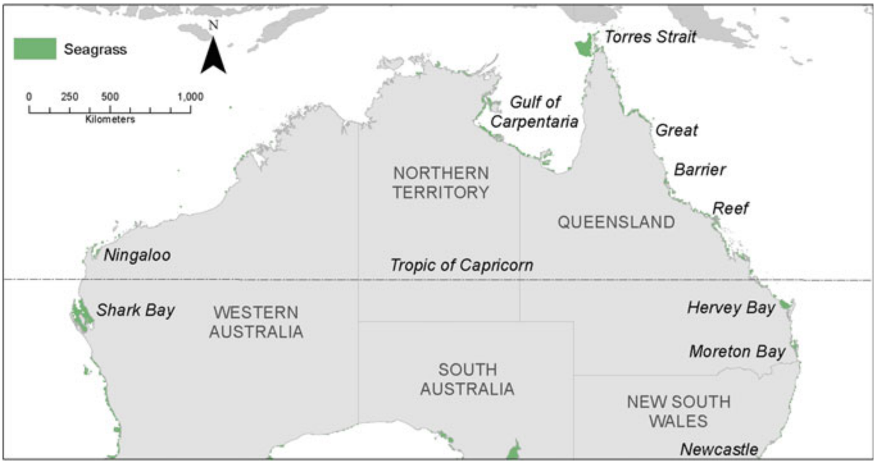

**Fig. 19.1** Map of northern Australia showing the known distribution of seagrasses. The winter range of the dugong extends from Shark Bay in Western Australian to Moreton Bay in Queensland. The summer range on the east coast extends south to Newcastle

## 19.2 Relationship Between Dugongs and Seagrass Communities

### *19.2.1 Which Seagrassses Do Dugongs Eat?*

Marsh et al. (2011) conducted a detailed audit of all records of dugong diet and concluded that dugongs feed on nine of the ten genera and probably on most of the approximately 26 species of seagrass that occur within their range (Green and Short 2003), with at least two likely exceptions: the robust, fibrous, temperate seagrasses *Posidonia australis* and *P. coriacea*, the ranges of which overlap the high latitude limits of the dugong's range in Western Australia.

Comparisons indicate that the relative importance of seagrass genera to dugongs differs among locations and may change at the same location during times of seagrass loss from plant dieback and extreme weather events. Dugongs expand their diet opportunistically in times of nutrient shortages, when seagrass beds are seriously depleted. For example, the relative importance of different seagrass genera in the stomach contents of dugongs changed during the year after the 1971 Townsville cyclone (Marsh et al. 1982). In addition, Preen and Marsh (1995) found algae, dead seagrass rhizomes and anoxic sediment in the stomachs of dugongs that died in the Hervey Bay region in south-east Queensland after the loss of more than 1000 km$^2$ of seagrass caused by two floods and a cyclone in 1992. Comparison of the diets of dugongs killed by indigenous hunters at Mabuiag Island in Torres Strait in 1977 (a time of seagrass dieback) and 1997–98 (when the seagrass beds were healthy) indicates that the dugongs ate relatively more of the fibrous species *Enhalus acoroides* when seagrass was scarce.

Dugongs may also change their diet on a seasonal basis. Such changes are most apparent at the high latitude limits of their range where access to some seagrass meadows is limited by the water being too cold for dugongs in winter. Anderson (1998) observed dugongs feeding on *Halodule uninervis* in Shark Bay in summer, and inferred from their behaviour that they fed on *Amphibolis antarctica* (Anderson 1982) and *Halophila spinulosa* (Anderson 1994) at other locations in Shark Bay in winter. Although *Zostera muelleri*[1] is not usually eaten in Moreton Bay, Queensland, Preen (1992) observed some dugongs feeding on the narrow-leafed morph of this species in winter, possibly because it grows near the passage leading from the bay to warmer, oceanic water. Preen (1992) also observed dugongs feeding on the thin-leafed morph of *Zostera muelleri* in spring when it was fruiting. Seasonal changes in diet are not limited to the subtropics; Johnstone and Hudson (1981) noted that the dugongs with algae in their mouths were sampled in winter in tropical Torres Strait.

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[1] Referred to as *Zostera capricorni*. *Zostera capricorni* is now regarded as a sub-species of *Zostera muelleri* and is referred to as *Zostera muelleri* throughout this document irrespective of the original reference.

It is very difficult to confirm diet selection in the wild, especially for herbivores such as dugongs where food quality is likely more important than food quantity and food availability changes with tide and season. Preen (1992) ranked the dugong's preference for seagrasses in Moreton Bay, Queensland, in summer and autumn (when the abundance of seagrass is greatest) on the basis of: (1) frequency of encounter with feeding dugongs in different seagrass communities, (2) the relative abundance of different seagrasses in areas accessible to dugongs, and (3) the signs left by feeding dugongs. His ranking was: (1) *Halophila ovalis* (most preferred), (2) *Halodule uninervis* thin-leaf morph, (3) *Syringodium isoetifolium*, (4) *Halodule uninervis* broad-leaf morph, and (5) *Zostera muelleri* broad-leaf morph.

This hierarchy of seagrasses as preferred food for dugongs is not consistent across all locations or times. *Zostera muelleri* appeared to be the main seagrass eaten by dugongs in the inshore waters of a significant dugong habitat, Shoalwater Bay, Queensland, in 1975, although there was some evidence that dugongs avoided dense old stands (Anderson and Birtles 1978). *Amphibolis antarctica* is almost certainly the seagrass eaten most often by dugongs in Shark Bay, the area that supports the second largest known dugong population (Marsh et al. 2002, 2011; Sobtzick et al. 2014). *Thalassia hemprichii*, a climax species (van Tussenbroek et al. 2006), appears to be the most important food of dugongs in Torres Strait, the area which supports the world's largest dugong population (Marsh et al. 2002, 2011). *Thalassia hemprichii* was found in the mouths of 73% of the dugongs from the Daru region of Torres Strait, a higher proportion than *Halophila ovalis* (67%) or *Halodule uninervis* (52%) (Johnstone and Hudson 1981). On the basis of stomach contents analysis, André et al. (2005) concluded that the dugongs caught by hunters in 1997–99 in the Orman Reef area of Torres Strait were mainly eating *Thalassia hemprichii*, *Cymodocea* sp. and *Syringodium isoetifolium*, the seagrasses which dominated the area in biomass. *Halophila ovalis* and *H. spinulosa* were consumed only incidentally despite being present at densities comparable to those in Moreton Bay, where Preen (1992) considered them preferred foods. *Enhalus acoroide*s was present in abundance in Torres Strait but was not targeted by dugongs in 1997–99, in contrast to the time of seagrass dieback in the mid-1970s (see Marsh et al. 2011).

Sheppard et al. (2010) conducted the most comprehensive study of factors influencing dugong diet selectivity. Their analysis was limited to a 24 $km^2$, intensively-used seagrass habitat in subtropical Hervey Bay, south-eastern Queensland, in winter where they tracked seven male dugongs at a fine spatial scale (<10 m) using GPS transmitters. They modelled resource selection within the habitat by comparing the dugongs' use of space (which they assumed was an index of their consumption of seagrass) with the species composition, biomass and nutrient characteristics of the seagrass landscape, which had been mapped in detail (Sheppard et al. 2007). Patterns of association between dugongs and the four seagrass species present, all of which were low biomass species, were complex and indefinite. Dugongs were associated with *Halodule uninervis* and *Halophila spinulosa* only on daytime low tides when the animals' habitat choices were limited by tides and possibly vessel traffic. The dugongs were associated with *Halophila ovalis* only at intermediate tides at night. In general the dugongs tended to avoid areas with a high density of *Halophila spinulosa* and *Zostera muelleri*. Sheppard et al.'s (2007) results are consistent with some of Preen's (1992) findings from Moreton Bay, but demonstrate that the selection of seagrass by dugongs is probably influenced by many factors other than the relative prevalence of seagrass species per se.

Anderson (1998), Masini et al. (2001) concluded that dugongs preferentially feed on *Halodule uninervis* to maximise energy intake because its rhizomes are rich in starch (see 'Food quality' below). While not eliminating this possibility, Sheppard et al. (2010) demonstrated that the situation is more complex at their study site in Hervey Bay. The association of dugongs with seagrasses high in starch was positive during both day and night high tides when the animals could access the intertidal areas where the seagrass biomass was generally low. Nonetheless, the researchers found that the tracked dugongs were consistently associated with seagrass patches where nitrogen concentrations were relatively high, except during the day at low tides when their choice was restricted. The dugongs then associated with seagrass patches of high biomass.

### 19.2.2 What Other Organisms in the Seagrass Community Do Dugongs Consume?

In some environments, dugongs apparently subsist largely on algae. Whiting (2002, 2008) documented dugongs that were closely associated for long periods with algal-covered, rocky reefs in the Northern Territory in tropical Australia. During times of apparent nutrient shortage, dugongs also deliberately eat invertebrates associated with seagrass meadows, at least at the subtropical limits of their range such as Shark Bay and Moreton Bay in Australia. Anderson (1989) reports that dugongs created circular craters as they foraged for thin-shelled burrowing mussels *(Botula vagina)* and possibly sea pens (*Virgularia*) in Shark Bay during winter. On the basis of direct observations of feeding trails and analysis of digesta, Preen (1995b) demonstrated that invertebrates such as ascidians (especially *Sycozoa pulchra*) and unidentified chaetopterid worms are an important part of the diet of dugongs in Moreton Bay, especially in early spring. There is no scientific evidence that dugongs deliberately feed on invertebrates in the tropics, although dugongs certainly consume invertebrates incidentally when feeding on whole seagrass plants (Preen 1992; Marsh et al. 2011). Tropical seagrass meadows are generally more diverse than tropical meadows (Green and Short 2003) and dugongs have more choices among seagrass species. Interestingly the subtropical zone, on the west coast of Australia, does not follow this global pattern, and seagrass diversity is higher compared to the tropics, so in this environment, dugongs have more choice.

We conclude that within their relatively specialised habitats of intertidal and subtidal tropical and subtropical seagrass meadows, dugongs are capable of exploiting a relatively wide diet including macro-invertebrates and algae. This capacity probably explains their large range. Thus we suggest that dugongs should be referred to as seagrass community specialists rather than seagrass specialists.

## 19.3 Seagrass as Food for Dugongs

### *19.3.1 Biomass*

The below-ground (below-substrate) biomass of seagrass of the seagrasses on which dugongs feed is generally much greater than the above-ground (above-substrate) biomass (see Marsh et al. 2011). The ranges of both the above-ground biomass (5–208 g ww $m^{-2}$) and the below-ground biomass (8–1330 g ww $m^{-2}$) are considerable (Marsh et al. 2011).

### *19.3.2 Food Quality*

Herbivores such as dugongs are faced with food that varies in quality as well as biomass. As pointed out by Aragones et al. (2006, 2012), a definitive set of determinants of food quality for dugongs is not yet available. The obstacles to assessing food quality more precisely require long-term experiments using captive animals, with diets varying in the components of interest, to measure relationships between diet and digestive efficiency, body condition and health, and other measures of performance.

Forage nutrients are conveniently divided into the components making up the structure of the plants (cell wall) and the nutrients contained inside the cell wall (cell contents). The cell content components studied in the plants eaten by dugongs have generally been protein, total nitrogen, water-soluble carbohydrate and starch. Nitrogen is a proxy for protein, whereas water-soluble carbohydrate is the most rapidly digestible part of the non-structural carbohydrate in plant tissues, and starch is the most important of the storage carbohydrates in plants (Aragones et al. 2006, 2012).

The components of plant cell walls are cellulose and hemicellulose and related polymers, principally lignin (Parra 1978). Herbivorous mammals such as dugongs do not produce the enzymes required to digest cellulose and other fibrous components of their diets (Van Soest 1994). Hence some portion of their digestive tract must be modified to contain the symbiotic organisms capable of hydrolysing the substances resistant to the digestive enzymes secreted by the host animal. In dugongs this portion of the digestive tract is the hindgut as discussed below.

Various biologists have measured the nutrients in some food plants of dugongs, especially seagrasses. Early assessments tended to be based on unreliable measures of food quality such as caloric value (e.g. Birch 1975). In recent years, researchers have used the more established chemical measures developed for domestic herbivorous mammals (for a discussion of methods see Van Soest 1994).

Near Infra-red Reflectance Spectroscopy, a widely accepted method for the determination of the chemical attributes of organic materials (Lawler et al. 2006), has also been used to study the nutrient qualities of seagrass as food for dugongs.

#### 19.3.2.1 Nitrogen

The structural building blocks of animal tissues are proteins, while in plants they are carbohydrates. Animal tissues are usually about 10% nitrogen, yet plant tissues are often as low as 1–2% nitrogen (Bentley and Johnson 1991). Consequently, nitrogen is often the dietary component in short supply for herbivorous mammals, particularly young growing animals and females in the late stages of pregnancy and lactation (Frape 2004). As hindgut fermenters, dugongs have fewer opportunities to capture the nitrogen synthesised by gut microbes than foregut fermenters like ruminants because most of their gut microbes are in the colon, relatively late in the gut passage (Van Soest 1994). So we might expect nitrogen to be a major limiting nutrient for dugongs, as suggested by Lanyon (1991).

Although nitrogen has not been confirmed as the major criterion for food selection by dugongs, some data support this hypothesis. As discussed above, Sheppard et al. (2010) reported that the dugongs they tracked (which were all males, rather than pregnant or lactating females or rapidly growing young calves with greater nitrogen needs) were consistently associated with foods with relatively high nitrogen concentrations, except at low tide when the availability of such food plants was limited. Both small and large groups of dugongs feed repeatedly on areas of seagrass (de Iongh et al. 1995, 2007; Preen 1995a) suggesting that they take advantage of the increased nitrogen concentrations in new growth, despite the concomitant decrease in starch (energy) (see 'dugong–plant interactions' below). The importance of *Thalassia* leaves (which are rich in nitrogen) to dugongs in Torres Strait, the region which supports more dugongs than anywhere else in the world, and the tendency of dugongs to feed opportunistically on animals as discussed above are additional arguments in favour of nitrogen being important for dugong nutrition.

The available data (Murray et al. 1977; Best 1981; Tucker and DeBusk 1981; Anderson 1986; Silverberg 1988; Duarte 1992; Aragones 1996; Sheppard et al. 2007, 2008) indicate that whole plant nitrogen levels for seagrasses and macroalgae are mostly 1–4% of plant dry matter [DM], within the range for horse forage (Frape 2004). The nitrogen concentration in seagrass leaves is often more than twice that of the rhizomes (Lanyon 1991; Aragones 1996; Sheppard et al. 2007, 2008), although *Halophila spinulosa* and *Syringodium isoetifolium* can be exceptions to this pattern. The nitrogen values for the leaves of various species of *Thalassia* (1.6–3% dry matter, van Tussenbroek et al. 2006) and *Halodule* (>1.9% DM; Lanyon 1991; Provancha and Hall 1991; Aragones 1996; Sheppard et al. 2007) are typically relatively high; *Amphibolis antartica* leaves are relatively low in nitrogen (~1–1.2% DM, Walker and McComb 1988).

The nitrogen content of seagrasses can vary based on a several factors. Firstly, as seagrasses can accumulate excess nitrogen and phosphorus in tissues, concentrations can be elevated when external supply is greater or other factors such as light are limiting growth (Touchette and Burkholder 2000; McMahon et al. 2013). Nutrient concentrations also tend to be lower during the peak growing season (McMahon 2005). Thus the concentrations of nitrogen in seagrasses are variable but are not dissimilar to those of some terrestrial grasses. As explained below, this generalisation could be negated by the fact that the values reported here represent total nitrogen, rather than digestible nitrogen.

Despite the arguments for the importance of nitrogen, de Iongh et al. (1995, 2007), de Iongh (1996), Anderson (1998), Masini et al. (2001) claim that dugongs favour foods rich in starch and water-soluble carbohydrates on the basis of their alleged preference for the rhizomes of *Halodule uninervis*. These claims ignore two salient facts: (1) relative to most other seagrasses, the leaves of *Halodule uninervis* are generally also rich in nitrogen (see below); and (2) the stomach contents of dugongs eating *Halodule* sp. contain a substantial proportion of leaves as well as rhizomes (Marsh et al. 1982). Nonetheless, it is likely that access to energy is more important to dugongs at some times of year and at some latitudes than others, making the energy from the starch in rhizomes relatively more important. The fact that seagrass leaves are generally richer in nitrogen and fibre whereas the roots and rhizomes are richer in non-fibrous carbohydrate confirms the advantage to dugongs of eating the leaves, roots and rhizomes of seagrass when they are accessible rather than the leaves only.

#### 19.3.2.2 Starch and Water Soluble Carbohydrates

Aragones (1996) measured starch and water-soluble carbohydrate in the above- and below-ground components of eight species of seagrass. Concentrations were always higher in the below-ground components with the exception of *Halophila spinulosa*, for which the starch concentration was higher in the leaves. Concentrations also vary seasonally, particularly in the rhizomes (Kraemer and Hansiak 2000) because carbohydrate content is often a reflection of the physiological status of the plant (McMahon et al. 2013) and its environmental conditions. Thus seasonal patterns are unlikely to be consistent across species, time or space (see also Sheppard et al. 2007, 2008). Nonetheless, Lanyon (1991), Aragones (1996) and Sheppard et al. (2007) all found that, relative to other species of seagrass, the roots and rhizomes of *Halodule uninervis* are consistently rich in non-structural carbohydrates, particularly starch: the total concentration of water-soluble carbohydrate and starch averages ~14% in rhizomes of this species (Aragones 1996). The rhizomes of *Syringodium isoetifolium* can also be rich in these components (average ~10%;

Aragones 1996) but the concentration of starch declines with depth (Sheppard et al. 2008). Sheppard et al. (2007) also found that total starch was higher in intertidal than subtidal *Zostera muelleri*.

#### 19.3.2.3 Structural Carbohydrate and Fibre

As discussed below, hindgut fermentation has been confirmed as an important source of energy in dugongs. Murray et al. (1977) measured high values for the products of fibre fermentation (volatile fatty acids or VFAs) in the caecum and colon of a dugong and Murray (1981) noted that the relative concentrations of the principal VFAs produced were typical of those of terrestrial ruminants feeding on highly fibrous diets. Goto et al. (2004a) used microorganisms obtained from the faeces of two captive dugongs to demonstrate degradation of *Zostera marina* in vitro. Thus we would expect the amount of structural carbohydrate or fibre in the diet of dugongs to be important (Van Soest 1994). The standard method developed by Robertson and Van Soest (1981) to analyse the fibre content of plant foods first measures neutral detergent fibre (NDF, essentially the cell wall and usually equated with this fraction). The neutral detergent residue is then subjected to acid detergent extraction. The resultant acid detergent fibre (ADF) comprises lignin, cellulose and cutin, the values of each of which can be sequentially estimated by further extraction. ADF is widely used as a quick estimate of the fibre content in feeds (Van Soest 1994). Hemicellulose (plus some protein attached to cell walls) is usually determined by the difference between ADF and NDF. Lignin is the most significant factor limiting the availability of nutrients in plant cell walls to animal herbivores because it is generally indigestible. Lignin gives rigidity to cell walls and is often used as a natural marker in digestive physiology (see ‘Digestion’ below).

Lanyon (1991) measured cellulose in four species of seagrass: values ranged from means of 13% Dry Matter (DM) in the roots and rhizomes of *Halophila ovalis* to 22% DM in the leaves of *Zostera muelleri*. These values are generally less than the fibre levels in the forage plants of terrestrial herbivores (Best 1981), presumably reflecting the reduced need for structural reinforcement for plants growing in water as Lanyon and Sanson (2006a) point out. The mean NDF concentrations in seagrass leaves range from means of 32% DM in *Halophila ovalis* to 63% DM in *Zostera muelleri* and are often higher than the corresponding values for rhizomes (Lanyon 1991; Aragones 1996; Sheppard et al. 2007, 2008). The differences among seagrass species are not always consistent, presumably reflecting the ages of the plants sampled. Typical NDF values for terrestrial grasses are in the 50–70% range, whereas browse values tend to be in the region of 30–50% (Van Soest 1982 in Duncan and Poppi 2008). Seagrass are clearly not more fibrous than terrestrial forage.

### 19.3.2.4 Secondary Metabolites

From a herbivore's perspective, the nutritional quality of a plant depends on its nutrient content and the ability of the animal to extract the nutrients. Plant secondary metabolites may reduce the availability of some chemical components of plants to herbivores and may constrain both reproductive fitness and habitat use (e.g. Foley and Moore 2005; DeGabriel et al. 2009). The role of these compounds in the foods eaten by dugongs has received limited attention.

### 19.3.2.5 In Vitro Dry Matter Digestibility (IVDMD)

IVDMD attempts to simulate the digestive processes of herbivorous mammals using the enzymes pepsin and cellulose, and potentially integrates the individual assays for the other dietary components. Aragones et al. (2006) consider IVDMD to be the most informative measure of fibre in the foods of dugongs. Aragones (1996) measured the IVDMD of the leaves, roots/rhizomes and whole plants of 10 seagrass species eaten by dugongs including two species of *Cymodocea*, five species of *Halophila*, *Halodule uninervis*, *Syringodium isoetifolium* and *Zostera muelleri*. The mean IVDMD estimates were mostly extremely high ($\geq$80% potentially digestible) and comparable to the values estimated for dugongs in vivo. The IVDMD values obtained by Sheppard et al. (2007, 2008) were generally somewhat lower than those of Aragones (1996) but still relatively high. The high IVDMD of *Z. muelleri* is noteworthy. Both Preen (1995b) and Lanyon and Sanson (2006a) commented on the relatively large fragments of this plant in the faeces of dugongs and have assumed that it is not as efficiently digested as other seagrasses. The discrepancy is probably due to the dugong's difficulty in masticating *Z. muelleri*, making it relatively less digestible in vivo than suggested by Aragones' (1996) in vitro measurements on material that had been ground by machine.

Sheppard et al. (2007) found that, because of the relatively low intraspecific differences in the nutrient composition of the seagrasses at Burrum Heads in Queensland, nutrients were concentrated or dispersed according to seagrass biomass. The only detectable influence of site on nutrient distribution was tidal exposure. Intertidal *Halophila ovalis* possessed a higher IVDMD than subtidal plants of the same species and total starch was also higher in intertidal than subtidal *Zostera muelleri*.

The nutritional basis of food selection by dugongs is clearly an important topic for further research. However, contrary to some of the literature (e.g. de Iongh et al. 2007), there is no basis for the claim that the seagrass forage eaten by dugongs is of poorer quality than that eaten by many wild, large, terrestrial, herbivorous mammals.

## 19.4 How Do Dugongs Eat and Process Seagrass?

### 19.4.1 Evidence of Feeding

Dugongs can remove substantial proportions of the above- and below-ground biomass of some seagrasses (see Marsh et al. 2011). They feed by excavating or cropping, depending on seagrass morphology and the nature of the sediment. When feeding on structurally small seagrasses in the genera *Cymodocea*, *Halophila*, *Halodule*, *Syringodium* and *Zostera muelleri* (thin-leafed morph), dugongs excavate the plant community as they swim forward, carving characteristic feeding trails in the sea bottom and creating clouds of sediment (Heinsohn et al. 1977; Anderson and Birtles 1978; Preen 1992; Anderson 1998; Marshall et al. 2003; Fig. 19.2). These feeding trails are usually 10–25 cm wide (roughly the width of a dugong's facial disk), serpentine, between 30 cm and several metres long and up to about 6 cm deep (Fig. 19.3; Heinsohn et al. 1977; Anderson and Birtles 1978; Preen 1992); dugong feeding scars can also be circular (Aragones 1994; A Preen personal communication 1999) or elliptical (Nakanishi et al. 2008). Circular and elliptical scars presumably result from the dugong digging at a single spot rather than moving forward during feeding. Preen (1992) found no correlation between the mean length of feeding trails and the density of seagrass shoots at four sites where shoot density ranged from 261–2950 shoots per m$^2$, but noted that where *Syringodium*

**Fig. 19.2** Dugong using oral disc to excavate seagrass. Ahmed M. Shawky photograph.

**Fig. 19.3** Dugong feeding trail in a *Halophila ovalis* meadow on the Moreton Banks, Moreton Bay, near Brisbane, Australia. Kathryn McMahon photograph

*isoetifolium* occurred at the exceptionally high density of ~8700 shoots per $m^2$, the trails were only 30–50 cm long. Dugong feeding trails are used both by scientists and indigenous hunters (Nietschmann 1984), as evidence of dugong feeding activity. Feeding trails are presumably more reliable as an index of feeding activity on species that are excavated rather than cropped.

When feeding on larger, more robust seagrasses or in compacted sediments, dugongs feed by cropping seagrass leaves. In Shark Bay Western Australia, Anderson (1982) reported that dugongs fed on *Amphibolus antarctica* by 'stripping' the leaves off the stems. In Thailand, dugongs feeding on *Enhalus acoroides* cut the seagrass leaves at a consistent above-ground height and tooth marks consistent with dugong teeth were seen on the leaves (Nakanishi et al. 2008). Examination of the stomach contents of dugongs feeding on *Thalassia hemprichii* and *E. acoroides* indicates that their rhizomes are not generally eaten (Erftemeijer et al. 1993; André et al. 2005; Domning and Beatty 2007), presumably because they are either too fibrous or extend too deep in the sediment (e.g. 6–12 cm) for a feeding dugong to disturb (Domning and Beatty 2007).

## *19.4.2 Food Acquisition*

Several aspects of the morphology of the skull and mouthparts of dugongs influence their capacity to acquire different foods. Dugongs have the most deflected snouts

($\sim 70°$) of the extant sirenians. This high rostral deflection enables dugongs to place their disk against the substrate while feeding (presumably an energetically advantageous position for a benthic forager.

Vibrissae or whiskers are specialised hairs, which most mammals use only to pick up tactile cues. Like other mammals, dugongs use their vibrissae to help them explore their environments (Marshall et al. 1998, 2000, 2003); and their elaborate facial musculature, lips and vibrissae to capture their food and their oral bristles and lips to introduce vegetation into the sides of the mouth though a series of cyclical manoeuvres (Fig. 19.2). Marshall et al. (2003) hypothesised that dugongs used their bristles in a biological disassembly line to excavate seagrass rhizomes and other benthic organisms, clean them of sediment and pass them into the mouth in a methodical, rhythmic and efficient manner. This mechanism is remarkably good at cleaning the sediment off the seagrass; several researchers have commented on how little sand is typically found in dugong digesta (e.g. Heinsohn and Birch 1972; Erftemeijer et al. 1993), except when they are suffering from food shortage (Spain and Heinsohn 1973; Preen and Marsh 1995). Domning and Beatty (2007) compared the stomach contents of dugongs with and without erupted tusks and by examining the geometry and micro-wear of worn tusks. They concluded that male dugongs with erupted tusks do not consume more rhizomes than females without erupted tusks and that tusks do not play a significant role in feeding in modern dugongs. Nonetheless, each tusk is worn laterally into a bladelike shape, presumably as the excavating dugong moves forward. Despite various claims, there is no evidence that the dugong uses its flippers to manipulate seagrass.

### 19.4.3 Seagrass Consumption

There are few reliable estimates of daily food intake in dugongs, all from captive animals. The most reliable as a wet weight percentage of body weight are 14.3% for a one year old calf and 7% for an adult, both feeding on *Zostera marina* (Goto et al. 2004b).

### 19.4.4 Mastication

Herbivores derive energy from plant material through the enzymatic breakdown of cell contents and the microbial fermentation of cell walls (Keys et al. 1969; Van Soest 1994). As explained in ‘Digestion’ below, dugongs are hindgut fermenters like horses and elephants, and rely on symbiotic organisms in the caecum and colon to ferment the fibrous portion of their diet. In herbivores, the rates of fermentation and enzymatic digestion are affected by the size of the food particles presented to the microflora (Clauss and Hummel 2005). Thus for a dugong to access the nutrients in its food optimally, plant material must be broken down mechanically into small fragments. Terrestrial grasses have abrasive particles of silica in their leaves and stems (McNaughton et al. 1985). In contrast, seagrasses, are not only less abrasive but are also much easier to rupture than terrestrial grasses (Lanyon and Sanson 2006a). Nonetheless, some abrasive particles of substrate may also be taken in and cause wear on the teeth when dugongs feed on seagrasses.

Dugongs have simple, peg-like molars with degenerate enameled crowns that wear quickly, exposing the much softer and less wear-resistant dentine. The dugong's last two molars are open rooted and grow throughout life. These ever-growing cylinders of dentine constitute the entire cheek dentition of most old adult dugongs (Marsh 1980). The dugong's flat-crowned teeth are probably not very efficient at grinding plants, and Lanyon and Sanson (2006b) believe that they play a relatively unimportant role in the mechanical breakdown of the dugong's seagrass food. Surprisingly, dugongs can reduce seagrass to fragments almost as small as those produced by horses chewing hay (Frape 2004). Marsh et al. (1999) and H. Marsh (unpublished) measured the size of fragments of seagrasses in the stomach contents of dugongs and West Indian manatees eating the same genera of seagrasses and showed that, despite its simple dentition, the dugong is at least as effective at masticating the leaves and rhizomes of *Halodule* and the leaves of *Thalassia* as the West Indian manatee, *Trichechus manatus*, which has a much more elaborate dentition (neither species eats *Thalassia* rhizomes as explained above). However, this finding does not mean that the teeth of dugongs are as effective as those of manatees in masticating seagrasses. The dentition of both dugongs and manatees is only a part of their masticatory apparatus; their entire oral cavity functions to break down their food. Both dugongs and manatees have well-developed horny pads or plates at the front of their mouths (Murie 1872; Gohar 1957). In addition, the palate of the dugong (but not of the Florida manatee) is modified into regions of horny papillae and folds (Marsh and Eisentraut 1984) that may assist in mastication. The relatively small dugong tongue is probably also important in positioning food in the mouth (Yamasaki et al. 1980; Levin and Pfeiffer 2002). Thus the sizes of the fragments in dugong stomachs reflect the relative effectiveness of their entire masticatory apparatus rather than the teeth per se.

Dugongs are less effective at masticating fibrous seagrasses (e.g. *Enhalus acoroides*, *Zostera muelleri*) than low-fibre seagrasses such as species of *Halodule* and *Halophila* (Marsh et al. 1982; Preen 1992; Lanyon and Sanson 2006a). Indeed Nakanishi et al. (2008) reported that when dugongs feed by cropping *Enhalus* the hard leaf edges, which remain as black fibres at the base of living plants, were left. The macroalgal fragments in dugong stomachs are also often large (Lipkin 1975; Marsh et al. 1982). These limitation to the masticatory apparatus of dugongs may be most important under lengthy periods of food scarcity, such as at times of seagrass dieback (Marsh and Kwan 2008) and may be one reason for the large temporal fluctuations in dugong fecundity discussed below.

### 19.4.5 Digestion

Herbivorous mammals such as the dugong do not produce the enzymes required to digest cellulose and other fibrous components of their diets (Van Soest 1994). Hence a region of their digestive tract must be modified to contain the symbiotic bacteria, protozoa and fungi capable of hydrolysing cellulose, hemicellulose and other substances resistant to their digestive enzymes. The principal organic end products of this fermentative digestion are Volatile Fatty Acids (VFAs), which herbivores absorb and use as energy sources (Parra 1978; Van Soest 1994).

The large intestine, and especially the colon, is the major fermentation chamber of the dugong and numerous species of bacteria have been cultured from the dugong hindgut (Goto et al. 2004a; Tsukinowa et al. 2008). When compared with most other colon fermenters, the gastrointestinal tract of sirenians is remarkable (Reynolds and Rommel 1996). The structural adaptations common to all sirenians include a discrete accessory digestive gland associated with the stomach, duodenal diverticulae and an exceptionally long and relatively narrow colon. This combination is unique. These features enable sirenians to process their food in a way that is different from most other colon digesters, which tend to consume bulky food at the expense of efficient fermentative action (Parra 1978; Van Soest 1994).

Murray et al. (1977) found that the concentrations of VFAs in the dugong's stomach were very low, demonstrating that it is not an important fermentation site. Lanyon and Sanson (2006b) measured the particle size of the digesta at various places along the alimentary tract of three dugongs and found that about 50% of the post-oral breakdown occurred in the stomach, presumably mostly as a result of the muscular contractions of the stomach wall. Taken together, these features suggest that the sirenian stomach is a site of water resorption and particle size reduction rather than nutrient absorption.

The dugong's small intestine is only half as long as the hindgut. Lanyon and Sanson (2006a) demonstrated that a further 25% of the post-oral reduction in the particle size of digesta occurs in the small intestine of the dugong. Murray et al. (1977) concluded that digestion in the dugong small intestine is negligible. The small intestine typically contains little digesta, suggesting a rapid passage rate (H. Marsh unpublished data). We conclude that the small intestine probably does not play a significant role in dugong digestion but is important in reducing the size of particles of digesta via muscular contractions.

The colon is a narrow tube up to 25 m long in a large dugong (>8 body lengths; Spain and Heinsohn 1975). The digesta retention time is unusually long. Clauss et al. (2007) reviewed the mean ingesta retention times of 93 herbivorous mammals including caecum and colon hindgut fermenters and ruminant and non-ruminant foregut fermenters. Only the three-toed sloth, *Bradypus tridactylus* (a non-ruminant foregut fermenter with a low metabolic rate), has been recorded as having a retention time comparable to that of dugongs and manatees.

Lanyon and Sanson (2006a) demonstrated that a further 28% of post-oral reduction in the particle size of digesta occurred in the caecum and large intestine of the dugong. The hindgut (caecum and colon) is the major site of fibre digestion and VFA production (Murray et al. 1977). Digestive efficiency is inversely correlated with gut passage rate (Clauss et al. 2007), so it is not surprising that the digestive efficiency of dugongs and manatees is very high relative to that of other herbivorous mammals, especially other hindgut digesters. Whereas their capacity to digest crude protein (nitrogen) is unremarkable, dugongs, like green turtles (Bjorndal 1980), digest a very high proportion of the fibre in their diet compared with other colon fermenters like the horse. This high digestive efficiency may explain the exceptionally high values for VFAs found by Murray et al. (1977) in the caecum and colon of a dugong. Despite these high values, Murray (1981) estimated that the VFAs would not contribute as much to the energy metabolism of a dugong as to terrestrial ruminants, which may be why dugongs also seek seagrasses high in starch and water-soluble carbohydrates.

## 19.5 Effects of Dugongs on the Seagrass Community

### *19.5.1 Responses to Dugong Grazing*

There is a large body of literature documenting the responses of plant communities to grazing by large terrestrial herbivores (e.g. Olff and Ritchie 1998; Bakker et al. 2006). The ecosystem effects caused by the feeding of dugongs are much less well understood. Nonetheless, seagrass scientists increasingly acknowledge the importance of herbivory in tropical seagrass ecosystems (Valentine and Duffy 2006) and that the local effects of dugongs on subtropical and tropical seagrass ecosystems can be significant. Supanwanid et al. (2001) review the methods for studying the effects of large herbivores on seagrasses. These effects have been studied empirically using several approaches: (1) observations of known feeding sites within meadows, typically including comparisons of undisturbed sites with sites where dugongs have fed and/or the same site over time (e.g. Wake 1975 in Heinsohn et al. 1977; Anderson and Birtles 1978; de Iongh et al. 1995, 2007; Preen 1995a, b; Peterken and Conacher 1997; Nakaoka and Aioi 1999; McMahon 2005); (2) comparisons among meadows with different intensities of dugongs feeding in the same general area (e.g. McMahon 2005); (3) field experiments in which sirenians were excluded from locations within seagrass beds (e.g. Preen 1995a; Masini et al. 2001; Burkholder et al. 2013); and (4) field experiments in which cropping and excavating have been simulated in seagrass beds (e.g. de Iongh et al. 1995, 2007; Supanwanid 1996; Aragones and Marsh 2000; McMahon 2005; Aragones et al. 2006).

The effect of dugongs feeding on seagrasses can be measured at several levels and by using different response variables, the levels include the individual feeding scar, the area disturbed per day by an individual animal, and the effect of a large group of animals on an individual plant community (Fig. 19.4). The response variables include: microbial processes, above- and below-ground plant biomass,

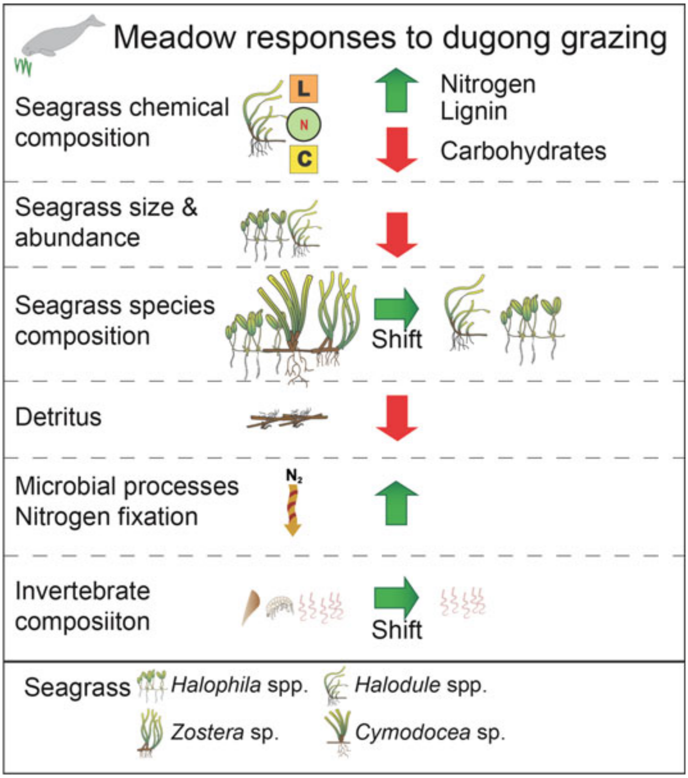

**Fig. 19.4** Diagrammatic representation of dugong seagrass interactions

plant species composition, plant nutrients, invertebrate community composition and detritus, plus the time taken by each of these variables to return to the pre-disturbed condition. We deal with each of these effects below.

#### 19.5.1.1 Microbial Processes and Detritus

Perry and Dennison (1996, 1999) showed that the rates of microbial nutrient cycling in seagrass sediments in subtropical Moreton Bay, Queensland, increased after intensive excavating by dugongs. The nitrogen fixation rates they measured in seagrass sediments disturbed by dugong feeding were the highest ever measured for a seagrass system. Perry and Dennison (1999) concluded that excavating dugongs aerate the substrate, fragment the seagrass releasing dissolved organic carbon and mix some of the detritus with sediment, producing a substrate for bacterial nitrogen fixation that apparently increased seagrass productivity.

Herbivory also alters the relative abundance of detrital (dead organic) matter in a seagrass meadow. Aragones and Marsh (2000) showed experimentally that intensive dugong excavating reduces detritus, presumably because most of the plant material is eaten rather than left to die and decay. In Moreton Bay, Queensland, McMahon (2005) also found more detritus in seagrass sediments in an area where dugongs rarely feed than in two areas where they furrowed intensively. Heinsohn et al. (1977) observed that dugongs avoided dense, old stands of *Zostera muelleri*; Preen (1992) noted that dugongs avoided seagrass with the high epiphyte loads that can be accrued over long periods without physical disturbance. Collectively these findings suggest that excavating dugongs increase the variation in the age structure of seagrass communities, thereby reducing the buildup of detritus.

#### 19.5.1.2 Seagrass Biomass and Productivity

As explained above, adult sirenians consume about 7% of their body weight per day; calves and juveniles consume relatively more, but in absolute terms less food (Marsh et al. 2011). Thus even an individual sirenian can disturb a considerable area of seagrass in a single day, especially in areas with low biomass. Preen (1992) assumed that an individual dugong consumed 3.22 kg dry weight/day and estimated that each dugong disturbed about 400 $m^2$ of seagrass each day in Moreton Bay, Queensland, where the median biomass was 12.3 g $DM/m^2$. In the Great Barrier Reef region, also in Queensland, where the biomass of the seagrasses on which dugongs feed ranges from 5.8 to 10.4 g dry $matter/m^2$, Marsh et al. (2005) estimated that each dugong would disturb about 300–800 $m^2$ of seagrass each day assuming a daily consumption of 3.16–4.52 kg dry matter.

The local impact on seagrass biomass can be very significant as explained in Sect. 19.1 above. McMahon (2005) monitored dugong feeding trails along a fixed 50 m transect in a *Halophila ovalis* meadow also in Moreton Bay where herds of 50–150 dugongs were regularly observed feeding. She observed dugong feeding trails in 11 out of 13 months and estimated removal of a monthly average of 23% of seagrass cover at the site. The highest percentage removed was in late winter (August) when the dugongs removed 65% of seagrass from the meadow. Masini et al. (2001) estimated that during the summer, an aggregation of dugongs feeding in a *Halodule–Penicillus* meadow in Shark Bay, Western Australia, caused a loss (ingestion plus drift) of over 50% of production. This value is similar to measures by McMahon (2005) in areas where the highest numbers of dugongs were observed in Moreton Bay, Queensland.

McMahon (2005) studied seagrasses at three meadows in Moreton Bay, Queensland, each of which represented a different level of intensity of natural dugong feeding on seagrass leaves, roots and rhizomes. Unfortunately, the levels of feeding were not replicated across meadows, making it impossible to unequivocally attribute the differences between meadows to differences in feeding intensity. McMahon found that *Halophila ovalis* growing in a meadow where dugongs intensively removed leaves, roots and rhizomes were twice as productive in summer and 1.5 times as productive in winter as plants of the same species growing in a meadow that was not disturbed by dugongs. This difference in productivity

(50–100%) between plants that are eaten and those that are not has not been replicated experimentally. The effect of sirenian feeding on plant productivity clearly requires further investigation.

#### 19.5.1.3 Community Structure and Composition

Field experiments demonstrate that feeding sirenians can have significant effects on the community structure and dynamics of multi-species seagrass meadows. Preen (1995a) conducted a simulated excavating and exclosure experiment in a community in Moreton Bay, Queensland, containing approximately equal proportions of *Zostera muelleri*, *Halophila spinulosa* and *Halophila ovalis*. Low intensity excavating did not alter the relative abundance of *Z. muelleri* or *H. spinulosa* and may have reduced the relative abundance of *H. ovalis*. In contrast, intensive excavating increased the relative abundance of *H. ovalis* at the expense of *Z. muelleri* and *H. spinulosa*. Aragones and Marsh (2000) simulated dugong feeding in a meadow at Ellie Point, in tropical Queensland, and found that both light and intensive excavating changed the species composition of the experimental plots in favour of *H. ovalis* at the expense of *Z. muelleri* and *Cymodocea rotundata*. Exclusion of dugongs resulted in increased *Cymodocea* seagrass and less *Halodule* in Shark Bay (Burkholder et al. 2013). All of these experiments demonstrate how dugong feeding can alter the composition of seagrass communities by favouring the growth of pioneer genera of seagrass such as *Halophila* and *Halodule.*

#### 19.5.1.4 Food Quality

The response of seagrasses to the short-term disturbance caused by feeding dugongs can also change the chemical composition of the plant material. Aragones et al. (2006) studied the responses of five species of seagrass to experimental removal, in a manner that simulated the two dugong feeding modes, of: (1) excavating seagrass leaves, roots and rhizomes; and (2) cropping leaves only. *Halophila* and *Halodule* were the main genera that showed interesting changes in nutritional qualities. The whole-plant nitrogen concentrations of *H. ovalis* and *H. uninervi*s increased by 35 and 25% respectively, even after nearly a year of recovery from intensive excavation of whole plants. These gains were tempered by a concomitant reduction in starch and increase in fibre concentrations. In the short term, the nitrogen concentrations increased whereas the fibre concentrations decreased. The proportion of new foliage with relatively less structural material increased after the above- and below-ground parts of the seagrass were removed, leading to increased nitrogen concentrations, whereas mobilisation of energy reserves for rebuilding the above-ground biomass led to reduced starch concentrations. As explained above, the lack of a definitive set of determinants for dugong food quality is a barrier to understanding the significance of these changes in the nutrient composition of seagrasses eaten by dugongs.

#### 19.5.1.5 Seagrass Population Dynamics

Dugongs have the potential to be biotic vectors for dispersal of seagrass seeds (McMahon et al. 2014; Tol et al. 2017). If dugongs feed on seagrass containing mature seeds, as has been observed by Peterken and Conacher (1997), they facilitate gene flow between dugong feeding areas via their faeces. Dugongs are known to make individualistic moves over spatial scales ranging from tens to hundreds of kilometres, and between feeding areas (Sheppard et al. 2006; Cope et al. 2015). Only seagrass species with a hard seed coat could be dispersed this way. A number of researchers have observed intact and viable seeds in dugong faeces (See Chap. 6), providing evidence that dispersal is possible, however, the significance of this dispersal mechanism is not known.

Grazing by dugongs also has the potential to affect the clonality and genetic diversity of seagrass meadows. Disturbance by feeding dugongs could create microsites for germination and establishment of seagrass seeds, which could increase the number of clones in a meadow and the genetic diversity of the meadow. Clonality and genetic diversity of seagrass meadows can be influenced by a number of historical and contemporary processes, and disentangling all these factors can be challenging. One study found that under very high and repeated grazing pressure, the clonal richness and genetic diversity of *Halophila ovalis* seagrass meadows was lower compared with meadows with lower levels of grazing or no dugong grazing (van Dijk personal communication 2015). This researcher postulated that repeated high intensity grazing may remove genotypes from a meadow, resulting in a lower clonal richness, and over generations there is more inbreeding due to the reduced population size, resulting in lowered genetic diversity. Under moderate levels of dugong grazing, which is typical over the range that dugongs feed, the clonal richness and diversity of *H. ovalis* meadows were similar to ungrazed meadows. Further work is required to gain a better understanding of the interaction between grazing by dugongs and seagrass population dynamics and connectivity.

#### 19.5.1.6 Benthic Animals

There have been few studies of the direct and indirect effects of dugong feeding on benthic animals in seagrass communities. Direct effects include the consumption of invertebrates and the disturbance of the sediment caused by digging up seagrasses. In addition, because the feeding scars remain for weeks or months while the seagrass recovers, it is possible that this disturbance may induce secondary indirect effects on the benthic community by altering habitat structure.

Preen (1995b) studied dugongs feeding on a stalked benthic colonial ascidian (*Sycozoa pulchra*) that was growing at densities of >3500 colonies per $m^2$ in subtropical Moreton Bay in spring. Dugongs removed 93% of the ascidian colonies from the feeding trails. Presumably dugong feeding was a major local impact on the ascidian community, although the effects were not studied. Nakaoka et al. (2002) and Skilleter et al. (2007) studied the community structure and abundance of benthic animals in *Halophila* dominated meadows in Thailand and Moreton Bay, Queensland respectively. The densities of most (but not all) groups of invertebrates were generally higher in intact vegetation than in actual (both studies) or simulated (Moreton Bay only) dugong feeding trails. The magnitude of the differences in density varied among functional groups and taxa and different groups responded differently to the effects of physical disturbance on the sediment and seagrass removal per se. Differences in invertebrate community composition were detected in both studies. These differences persisted for at least weeks after the creation of the trails. Longer-term studies are required to understand how sirenian feeding affects benthic communities in a range of seagrass communities.

## 19.6 Recovery of Seagrass Communities from Dugong Feeding

Even the most intense and sustained removal of seagrass leaves, roots and rhizomes by dugongs leaves relatively small spaces (<1 m) between surviving tufts of seagrass (Preen 1995a), allowing recovery to occur by clonal growth, augmented by sexual reproduction in at least some species (e.g. *Zostera muelleri*, Peterken and Conacher 1997). McMahon (2005) conducted the most comprehensive study of the factors enabling *Halophila ovalis* to cope with dugong feeding disturbance. She concluded that fast growth, flexible clonal reproduction, regular and flexible sexual reproduction, and a persistent and abundant seed bank were all important to rapid recovery.

Recovery from feeding can be examined at the scale of a feeding trail, patch (group of feeding trails) or meadow, and can be measured in terms of cover, biomass or shoot density. The time scales of recovery of seagrass beds from dugong feeding depend on many factors including the intensity, nature, frequency and timing of the impact, its location within the meadow, the nature of the seagrass community, latitude and availability of light, as well as other factors which limit seagrass growth, such as nutrients. *Halophila ovalis* can recover very rapidly from the removal of leaves, roots and rhizomes by dugongs. McMahon (2005) concluded that this rapid recovery rate most likely results from rapid clonal growth. Recovery times of a month or less have been recorded in both the subtropics and tropics, for example by Nakaoka and Aioi (1999) in Thailand and McMahon (2005) in Moreton Bay, Queensland. Seagrasses other than the species of *Halophila* generally take longer to recover. de Iongh et al. (1995) estimated that the biomass of *Halodule uninervis* took five months to recover from dugongs removing leaves, roots and rhizomes in Indonesia in the wet season and did not recover at all during the dry season. Aragones and Marsh (2000) showed experimentally that recovery times ranged from months for *Zostera/Cymodocea* and *Halophila ovalis* at one location in tropical north Queensland to more than a year in a monospecific meadow of *Halodule uninervis* at another site in the same general area.

The speed and nature of seagrass recovery from dugong feeding clearly varies with time of year and location (Supanwanid 1996; Aragones and Marsh 2000; McMahon 2005). As Aragones et al. (2006) point out, the variable times taken for seagrasses to recover from dugong feeding indicate that the appropriate timing for dugongs to revisit sites is also likely to vary greatly in both time and space. Thus it is not surprising that there is considerable variability in feeding patterns and the return times to particular locations (e.g. Preen 1995b; de Iongh et al. 1995, 2007; Anderson 1998; Masini et al. 2001; Hodgson 2004; McMahon 2005). There are so many variables associated with environmental and anthropogenic changes to seagrass beds that reliable predictions of seagrass recovery and dugong return times may be impossible.

Seagrass meadows have variable recovery potential due to changeable light levels and seed availability both spatially and temporally (Rasheed et al. 2014). Understanding inter- and intra-specific differences in seagrass recovery and how this interacts with location will be critical to predict the consequences of climate events on dugongs and their sub-tropical and tropical seagrass habitats in the face of the increased frequency of severe storms predicted as a consequence of climate change (see Chap. 21, this volume).

## 19.7 Feeding Optimization?

The studies of the interactions between dugongs and seagrasses clearly demonstrate that they can have significant effects on the biomass, community structure and chemical composition of their food plants. Preen (1992, 1995b) coined the term ‘cultivation grazing’ for the apparently beneficial effects (from the dugongs’ perspective) that dugongs feeding in large herds had on the seagrass community. de Iongh et al. (1995, 2007) showed that this effect was not limited to dugongs feeding in large herds and even small groups of dugongs repeatedly return to the same areas. de Iongh (1996) speculated that the resultant increase in food quality (higher IVDMD) that he measured compensated for the lower intake per bite resulting from the reduced standing crop caused by frequent feeding.

The concept of resource management such as ‘cultivation grazing’ by terrestrial vertebrates is contentious because it tends to invoke group selectionist arguments. Gordon and Lindsay (1990) conclude that herbivorous mammals are very unlikely to actively manage their food resources unless individuals exhibit long-term territoriality or use exclusive home ranges. Dugongs have apparently not adopted either of these social systems (Marsh et al. 2011). Thus the use of the term ‘cultivation grazing' sensu Preen (1995a) is criticized by some ecologists. Nonetheless, like some large terrestrial herbivores and green turtles, dugongs apparently return to 'traditional' feeding sites, thereby maintaining 'grazing' or 'browsing lawns' sensu McNaughton (1984), Skarpe and Hester (2008) or at least local feeding patches of relatively young food plants of improved food quality (particularly through increased nitrogen and lower fibre content).

In terrestrial systems, herbivory may provide positive feedback to the plants via local scale inputs of faecal and urinary material (Augustine et al. 2003). Aragones et al. (2006) postulated that the feedback loop might be different with dugong herbivory, as the nutrients are likely to be moved away by water currents. However, McMahon (2005) provided evidence that *Halophila ovalis* plants were using nitrogen from dugong faeces at certain times of the year, because the nitrogen isotope signature of the plants in grazed meadows was close to that of dugong faeces. Perry and Dennison (1999) attributed the higher shoot nitrogen they observed in meadows of *Zostera muelleri* and *Halophila ovalis* where dugongs had removed seagrass leaves, roots and rhizomes to microbial nitrogen fixation stimulated by feeding dugongs. They suggested that a positive feedback would occur via the enhancement of the detrital cycle caused by the activity of nitrogen-fixing bacteria. These three studies show that there are a number of possible feedback loops in the dugong–seagrass ecosystems, which clearly warrant further investigation.

## 19.8 Competition with Green Turtles

Dugongs share seagrass meadows with green turtles, sometimes at locally high densities. André et al. (2005) compared the stomach contents of sympatric dugongs and green turtles caught by an indigenous fishery on the Orman Reefs in Torres Strait between Australia and Papua New Guinea. They found that dugongs fed exclusively on seagrasses (mainly the leaves of *Thalassia hemprichii*, and the leaves and rhizomes of *Cymodocea* spp. and *Syringodium isoetifolium*) whereas turtles consumed both seagrasses (especially the leaves of *Thalassia* and the fibrous *Enhalus acoroides* [usually avoided by dugongs]), and macroalgae (mainly *Hypnea* spp., *Laurencia* and *Caulerpa* spp.). *Thalassia*, the most abundant seagrass in the area, was the only overlap in the diets of the two species. However, the overlap would presumably have been greater in the same area at a time of seagrass dieback in the 1970s when dugongs consumed relatively more *Enhalus* (see Nietschmann 1984). André et al. (2005) concluded that a comprehensive study of food partitioning between dugongs and green turtles would require a detailed and concurrent study of the food resources and the animals' movements.

## 19.9 Interactions Between the Status of Seagrass Communities and Dugong Life History

Marked temporal fluctuations have been documented in several dugong life history parameters including: mortality, pregnancy rate, the age at first reproduction in both sexes, the size at which sexual maturity is reached (Marsh and Kwan 2008; Marsh et al. 2011) and the incidence of reproductively active males (Marsh 1995 but see Kwan 2002). These fluctuations seem to track major changes in the seagrass communities on which dugongs depend for food. These communities are subject to episodic diebacks that are often associated with extreme climatic events (Johannes and MacFarlane 1991; Preen and Marsh 1995; Poiner and Peterken 1996; Marsh and Kwan 2008; Rasheed et al. 2014).

Dugong mortality is affected by seagrass loss associated with local scale climatic drivers. Meager and Limpus (2014) analysed a 17 year data set of records of marine mammal strandings over a latitudinal gradient of 13° (>2000 km of coastline) on the urban east coast of Queensland. Peak mortality of dugongs (and inshore dolphins) followed sustained periods of elevated freshwater discharge (9 months) and low air temperature (3 months). The density and species composition of seagrass communities in inshore waters are closely related to freshwater discharge (Campbell and McKenzie 2004; Collier et al. 2012), with significant loss and declines of seagrasses following major discharge events (Wooldridge 2016).

When their food supply fails, individual dugongs variously exhibit one of two functional responses (Marsh et al. 2011). They may emigrate from the affected area or remain, consuming any remaining seagrass and low-quality food such as algae, and postpone breeding. Twenty-one months after the two floods and a cyclone in early 1992, the standardised index of the relative abundance of the dugong population of the Hervey Bay region in south-east Queensland was reduced to an estimated 500 ± SE 126 animals from an estimated 2206 ± SE 420 animals in 1988 (Preen and Marsh 1995). Although unprecedented numbers of dugong carcasses were found along 1500 km of coastline in 1992 and 1993, the dugong population of Hervey Bay recovered too fast for this population reduction to be caused by mortality in the absence of substantial temporary immigration, reaching 2547 ± SE 410 in 2005 (Marsh et al. 2006).

In the southern hemisphere summer of 2010/2011 Queensland, Australia experienced a series of extreme weather events driven by one of the strongest La Niña weather systems ever recorded with prolonged rainfall and flooding and three severe tropical storms that directly affected the north Queensland coast over the summer of 2010/2011: Tropical Cyclone (TC) Tasha (December 2010), TC Anthony (January 2011) and TC Yasi (February 2011). TC Yasi was a category five cyclone (the most severe category possible) and approximately 98% of intertidal seagrass area was lost in the regions directly affected by its path, and only a few isolated shoots remained in many coastal and reef habitats where long term seagrass cover assessments were conducted (McKenzie et al. 2012).

This unprecedented extreme weather followed above average rainfall associated with La Niña conditions in three of the four preceding summers and the seagrass was already in poor condition (McKenzie et al. 2012). The estimated size of the dugong population in the Southern Great Barrier Reef Region in November 2011 was the lowest since the time series of aerial surveys began in 1986 (Sobtzick et al. 2012) presumably reflecting both mortality (the dugong mortality recorded in the stranding records in 2011 was the highest on record; Meager and Limpus 2014) and temporary immigration.

The strongest evidence for fluctuations in the dugong's reproductive rate comes from Torres Strait (Marsh et al. 2002, 2011). Information on dugong life history was acquired from specimens obtained from dugongs as they were butchered for food by indigenous hunters at two major dugong hunting communities in Torres Strait: Daru in 1978–82 (a time of seagrass dieback and recovery) and Mabuiag Island in 1997–99 (when seagrasses were abundant) (Marsh and Kwan 2008). Dugongs sampled in 1997–99 had their first calf at younger ages (minimum of 6 cf. 10 years) and more frequently than those sampled some 20 years before (Marsh et al. 2011). Pregnancy rates increased monotonically during 1978–82 (Marsh et al. 2011), coincident with seagrass recovery. The age distribution of the female dugongs collected in 1997–99 at Mabuiag Island also suggested a low birth rate between 1973 and 1983 and/or a high level of mortality for calves born during that period (Marsh and Kwan 2008).

These results suggest that the life history and reproductive rate of female dugongs are adversely affected by seagrass loss (see also Fuentes et al. 2016). The accounts of Bernard and Judith Nietschmann, who spent a year on Mabuiag Island studying dugongs beginning in July 1976 (Nietschmann and Nietschmann 1981; Nietschmann 1984) and the oral history evidence recorded by Johannes and MacFarlane (1991) indicate that a high proportion of dugongs caught in Torres Strait during the 1970s were lethargic, with limited and poor-tasting fat. The Islanders refer to such dugongs as 'wati dangal' (lean dugongs with poor-tasting meat). The Islanders attributed this unusually high proportion of 'wati dangal' to inadequate food availability (Johannes and MacFarlane 1991). This conclusion is supported by the oral history evidence of Islanders and the observations of Nietschmann (1984) that the stomach contents of the 'wati dangal' he collected contained larger amounts of brown and green algae than the largely seagrass-eating 'malu dangal' (deep water dugongs which are fatter and considered good eating by Islanders). As discussed above, evidence from other areas suggests that dugongs eat algae and more fibrous species of seagrass in greater quantities when seagrass is in short supply (Spain and Heinsohn 1973; Marsh et al. 1982) and that they are not well adapted to using algae or fibrous seagrasses as a food source (Marsh et al. 1982). The seagrass in Torres Strait allegedly recovered in the early 1980s, coincident with the increase in the dugong reproductive rate and in the proportion of reproductively active males (Marsh 1995) and was in good condition when Kwan (2002) collected her samples in the late 1990s (Long and Poiner 1997; Taranto et al. 1997).

Dugongs in poor condition are unlikely to breed. The Islanders claim that the females in the best condition are either pregnant or are those seen mating, feeding or travelling with a male (Nietschmann and Nietschmann 1981). Marsh and Kwan (2008) showed that the mean fat thickness differs significantly among female reproductive classes. Pregnant females were fatter than all other reproductive classes, providing empirical confirmation of Islander traditional knowledge.

The dugongs that stayed in Hervey Bay after the extreme weather events in 1992 also delayed breeding and/or suffered high calf mortality. The proportion of the dugong population classified as calves during aerial surveys declined from 22% in 1988 to 2.2% in 1993 and 1.5% in 1994 (Preen and Marsh 1995) suggesting that the impacts of habitat loss on fecundity/calf survivorship may last several years. The percentage of calves then increased concomitant with the seagrass recovery, reaching 14.5% in 1999 (Marsh and Lawler 2001).

No calves were seen in the Southern Great Barrier Reef during the November 2011 dugong aerial survey. In contrast, the proportion of calves in Hervey Bay (9.7%; 2011) and Moreton Bay (8.5% in 2011 and 9.8% in 2013 were within the range expected for ‘normal conditions’ (Sobtzick et al. 2012, 2015). These regional differences reflect both the recent history of seagrass condition in the region and the nature of the extreme weather events in the summer of 2010–11. The seagrasses in the Southern Great Barrier Reef had been in decline for several years before the floods and cyclones of the summer of 2010–2011 and were considered ‘vulnerable’ (McKenzie et al. 2012) with declining trajectories. In contrast, the seagrass on the Eastern Banks in Moreton Bay had been in ‘Excellent’ condition (Healthy Waterways 2011) before the January 2011 flood. Even though the water quality in more than half the zones in Moreton Bay remained the same or declined after the flood, the Eastern Banks, which are habitat for most of the dugongs, declined only from Excellent to Excellent Minus due to increased algae and some decrease in water quality with some loss of seagrass. Nonetheless, Lanyon et al.’s (2011) health assessments of dugongs in this region eight months after the floods found that 17% of the animals they sampled in Moreton Bay were in poor (thin) condition, however, this decline in health, did not result in decreased calf counts in 2011 or 2013 (Sobtzick et al. 2015).

## 19.10 Managing Seagrass Beds as Habitats for Dugongs

In addition to climatic drivers, tropical seagrasses in northern Australia are affected by human impacts. Grech et al. (2011) identified these as poor quality terrestrial runoff from agricultural, urban and industrial land use (Orth et al. 2006; Coles et al. 2007); urban, industrial and port infrastructure development (Grech et al. 2011); dredging (Erftemeijer and Lewis 2006; York et al. 2015); commercial and recreational boating; and commercial shrimp (prawn) trawling. The individual pressures exerted by activities (e.g. loss of light, siltation and smothering caused by dredging) aggregate in time and space and result in a cumulative impact on seagrass habitats.

Grech et al. (2011) identified seagrass meadows of greatest risk to the cumulative impact of multiple activities in the Great Barrier Reef as those adjacent to large urban centres and ports. Other studies that cover both the marine (Halpern et al. 2008, 2015) and terrestrial (Visconti et al. 2011) biomes also find a positive correlation between human population density and cumulative impact.

The Australian Government's White Paper on Developing Northern Australia presents a plan for growth in food and agribusiness and resources and energy across the tropics (Australian Government 2015). Implementing the plan requires rapid population growth across the region, and the White Paper predicts a total population of 4–5 million by 2060. Coastal development (e.g. ports), the conversion of catchments to agricultural land use, and growth in shipping and boating traffic and human population across northern Australia will increase human pressures and cumulative impact on coastal seagrasses (Wooldridge 2016). Such an increase in pressures will reduce the capacity of seagrasses to withstand the impacts of climate change (Wooldridge 2016), including increasing sea and air temperatures, the increased magnitude of tropical storms and cyclones, extreme El Niño related events, and rising sea levels (Coles et al. 2015). The future of tropical seagrass habitats, and hence dugongs as seagrasses community specialists, will be determined by the capacity of local, State and Federal environmental management programs to minimize the impact of growth and development on coastal ecosystems.

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# Part VII
# Pollution and Global Climate Change

# Chapter 20
# Decline and Restoration Ecology of Australian Seagrasses

**John Statton, Kingsley W. Dixon, Andrew D. Irving,**
**Emma L. Jackson, Gary A. Kendrick, Robert J. Orth**
**and Elizabeth A. Sinclair**

**Abstract** Since the first version of this book almost 30 years ago, significant losses of seagrass meadows have continued to be reported from around Australia as a result of natural and human induced perturbations. Conservative estimates indicate losses over the past two decades have more than doubled that estimated in the late 1990s. Conservation and mitigation of disturbance regimes have typically been the first line of defence, but ecological restoration or intervention is becoming

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increasingly necessary in a rapidly changing environment, and is potentially a more effective management strategy where seagrass habitat is already lost or heavily degraded. Accordingly, there has been an increase in the number of restoration studies and projects feeding our knowledge-base of restoration practice across Australia. Yet despite this increase, successful restoration has been rare, often uncoordinated, and almost always at a scale that is orders of magnitude lower than the scale of loss. Clearly, our understanding of the ecological mechanisms underlying successful and unsuccessful seagrass restoration is not keeping pace with the rates of loss and societal needs for restoration. Indeed, many orders of magnitude more restoration effort, in terms of science and practice and their interactions, will be required to prevent further seagrass loss. The science of seagrass restoration or restoration ecology is still a young science, but has strong foundations built from several decades of ecological research addressing many aspects of ecological interactions in seagrasses. While restoration has strong scientific underpinnings from ecological theory, it is clear that restoration ecology can also contribute to ecological theory by providing new and novel opportunities to advance our understanding of the mechanisms that promote functional ecosystems. In this chapter, we provide examples of this understanding across the levels of biological hierarchy, from genes to landscapes, and where possible include future strategic research directions.

## 20.1 Decline of Australian Seagrasses

Great losses of seagrass meadows have continued to be reported from around Australia as a result of natural and human induced perturbations since the first edition of this book (Larkum et al. 1989). The majority of these losses have occurred along the heavily populated eastern Australian coastline of Queensland and New South Wales, and mid-western region of Western Australia (Fig. 20.1). Previous estimates of seagrass losses range from 45,000 ha (Walker and McComb 1992; based on 11 sites across Australia) to 145,000 ha (Kirkman 1997; 100,000 ha from natural causes). The latter represents 3% of the 5 million ha of Australian coastal and nearshore waters that seagrass are estimated to cover (Kirkman 1997). More recent reports (Table 20.1) suggest an additional 130,500 ha of seagrass cover has been lost since the 1999 estimate (Thomson et al. 2015; Fraser et al. 2014). Subsequently, Australia has recorded 5.5% loss of seagrasses since the 1930s. This represents observed and/or reported losses at specific sites, and therefore could still be a conservative representation of overall losses. However, they do not take into account seagrass recovery or seasonal variability, which can be considerable (see Ball et al. 2014).

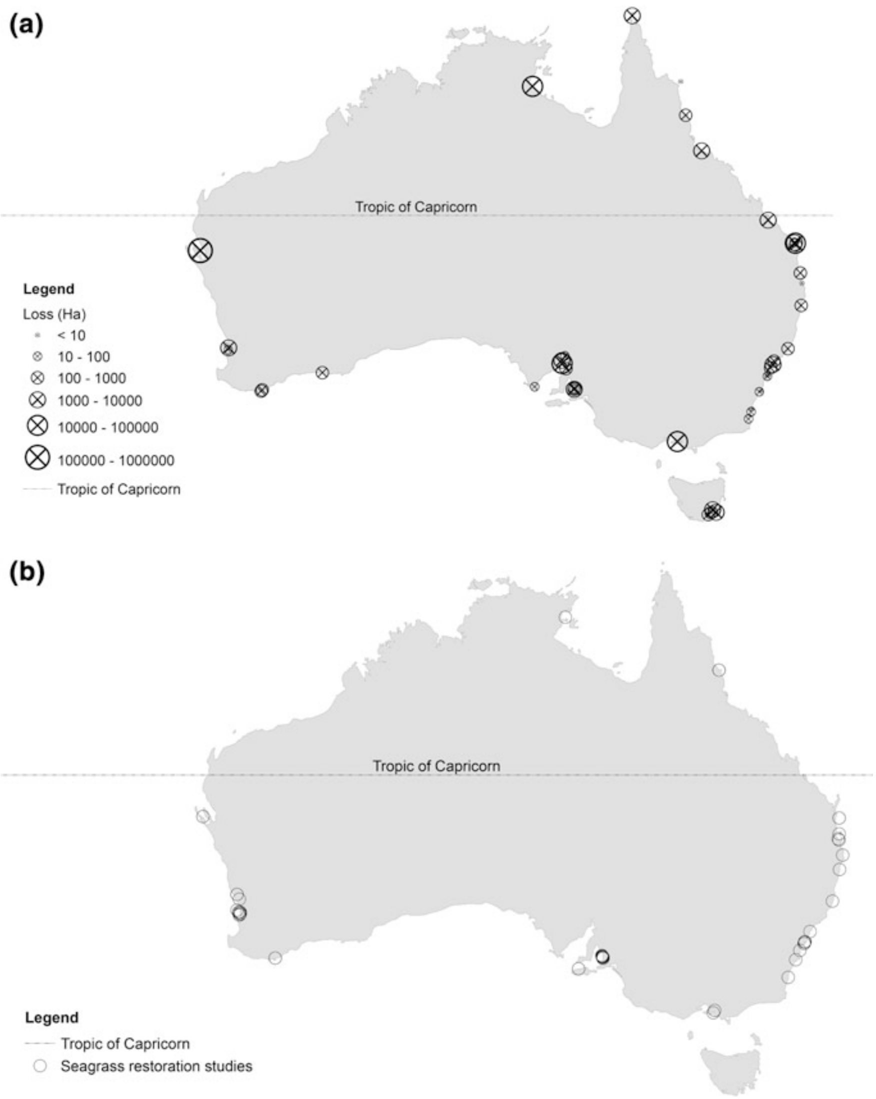


**Fig. 20.1** **a** Reported spatial losses of seagrass in Australia between 1930 and 2015 and **b** locations of seagrass restoration activities

The largest losses (in terms of rate of loss) have been recorded from the tropics and subtropics. In 1985, Cyclone Sandy destroyed over 18,300 ha of seagrass from West Island to Limmen Bight, Northern Territory (Poiner et al. 1987), although 10 years later the meadows have largely recovered. Transitory meadows of

**Table 20.1** Reported losses of seagrass in Australia since the 1930s

| Timeframe | Location | Area of loss (ha)[a] | Species | Drivers of loss | Reference |
|---|---|---|---|---|---|
| *New South Wales* | | | | | |
| 1930–1999 | Gunnamata Bay | 16 | *Posidonia australis, Zostera muelleri* | Severe storms; Bait digging; | Williams and Meehan (2001) |
| 1930–1985 | Botany Bay | – | *Posidonia australis* | Catchment management; Grazing (sea urchin) | Larkum and West (1990) |
| 1942–1999 | Burraneer Bay | 5 | *Posidonia australis, Zostera muelleri* | Dredge disposal | Williams and Meehan (2001) |
| 1942–1999 | Cabbage Tree Basin | 12 | *Posidonia australis, Zostera muelleri, Halophila* sp. | Sand migration | Williams and Meehan (2001) |
| 1948–1994 | Merimbula Lake | 47 | *Posidonia australis* | – | Meehan (1997) |
| 1951–1999 | Lilli Pilli Point | 7 | *Posidonia australis, Zostera muelleri* | Channel Dredging and sand migration | Williams and Meehan (2001) |
| 1951–1999 | Red Jacks Point | – | *Posidonia australis* | Shell grit excavation | Williams and Meehan (2001) |
| 1957–1994 | Wagonga Inlet | 8 | *Posidonia australis* | – | Meehan and West (2002) |
| 1957–1998 | Bermagui River | 14 | *Posidonia australis* | – | Meehan and West (2002) |
| 1960–1989 | Jervis Bay | – | *Posidonia australis* | Seismic testing | West et al. (1989) |
| 1961–1998 | St Georges Basin | 86 | *Posidonia australis* | – | Meehan and West (2002) |
| 1981–1997 | Brisbane Waters | 258 | – | – | Williams et al. (2003) |
| 1988–1995 | Wallis Lake | 518 | *Posidonia australis* | – | Dekker et al. (2005) |
| ____–1986 | Lake Macquarie | 700 | *Zostera capricorni*[b], *Halophila ovalis, Ruppia megacarpa* | Light reduction (eutrophication) | King and Hodgson (1986) |
| ____–1986 | Tuggerah Lakes | 1,300 | *Zostera capricorni*[c], *Halophila ovalis, Ruppia megacarpa* | Light reduction (eutrophication) | King and Hodgson (1986) |
| *Northern Territory* | | | | | |
| 1985–1985 | West Island—Limmen Bight | 18,300 | *Halodule uninervis*; *Halophila ovalis*; *Syringodium isoetifolium*; *Cymodocea serrulata*; *Halophila spinulosa* | Cyclone Sandy | Poiner et al. (1987) |

(continued)

**Table 20.1** (continued)

| Timeframe | Location | Area of loss (ha)[a] | Species | Drivers of loss | Reference |
|---|---|---|---|---|---|
| 1991–1992 | Torres Strait | 10,000 | *Halodule uninervis*; *Halophila ovalis*; *Syringodium isoetifolium*; *Cymodocea serrulata*; *Halophila spinulosa* | – | CSIRO study reported in Kirkman (1997) |
| *Queensland* | | | | | |
| 1992–1993 | Hervey Bay | 100,000 | *Zostera capricorni*[b] | Flooding; cyclone | Preen et al. (1995) |
| 1995–2012 | Lizard Island | 8 | *Thalassia hemprichii, Halodule uninervis* | Eutrophication | Saunders et al. (2015) |
| 1998–2001 | Urangan | 91 | *Zostera capricorni*[b] | – | Campbell and McKenzie (2004) |
| 1998–1999 | Wanggoolba Creek | 120 | *Zostera capricorni*[b] | – | Campbell and McKenzie (2004) |
| 1998–2002 | Northern Great Sandy Strait | 1,896 | *Zostera capricorni*[b] | – | Campbell and McKenzie (2004) |
| 2001–2013 | Townsville | 3,700 | *Zostera muelleri, Halophila ovalis, Halophila spinulosa* | Cyclone | Coles et al. (2015) |
| 2002–2013 | Gladstone | 1,600 | *Zostera muelleri, Halophila ovalis, Halodule uninervis* | Flooding, dredging, land reclamation | Coles et al. (2015) |
| 2004–2012 | Hay Point | | *Halophila decipiens* | Dredging Change in rainfall patterns | York et al. (2015) |
| 2007–2011 | Southport Broadwater Parklands | 1 | *Zostera muelleri, Halophila ovalis* | Land reclamation | Hall (2011) |
| 2007–2013 | Cairns | 700 | *Zostera muelleri, Halophila ovalis* | – | Coles et al. (2015) |
| 2007–2007 | Broadwater | 1 | *Zostera muelleri, Halophila ovalis* | Land reclamation | BIOME (2007) |
| ____–1990 | Moreton Bay | 257 | *Zostera capricorni*[b] | Sediment burial | Kirkman (1978) |
| *South Australia* | | | | | |
| 1908–1914 | Port Broughton | 320 | *Posidonia australis, Posidonia sinuosa* | Fibre harvesting | Irving (2013) |

(continued)

**Table 20.1** (continued)

| Timeframe | Location | Area of loss (ha)$^a$ | Species | Drivers of loss | Reference |
|---|---|---|---|---|---|
| 1932–1975 | Proper Bay | 38 | *Posidonia australis* | Nutrient enrichment (meat-works discharge) | Shepherd (1986) |
| 1939–present | Whyalla | 2,000 | *Posidonia* | Channel dredging; industrial discharge (ammonia) | Shepherd (1986), Harbison and Wiltshire (1993) |
| 1949–1995 | Adelaide | 4,000 | *Posidonia sinuosa, Amphibolis antarctica* | Eutrophication | EPA (1998) |
| 1967–1967 | Mambray creek to Douglas Point | 14 | *Posidonia australis* | Pipeline construction | Irving (2014) |
| 1978–1985 | Gulf of St Vincent | 365 | *Posidonia* spp., *Amphibolis* spp. | Sewage outfall<br>Eutrophication | Neverauskas (1987) |
| 1993–1993 | Spencer Gulf | 12,717 | *Amphibolis antarctica and intertidal Zostera* spp. | Thermal stress | Seddon et al. (2000) |
| _____–1985 | Holdfast Bay and off Bolivar | 5,222 | *Posidonia sinuosa, Posidonia angustifolia, Amphibolis antarctica* | Light reduction<br>Increased epiphytism<br>Eutrophication | Neverauskas (1987) |
| _____–1988 | South of Outer harbour, Holdfast Bay | 100 | *Posidonia sinuosa* | Sediment burial | Sergeev et al. (1988) |
| _____–1988 | Holdfast Bay | – | *Posidonia sinuosa, Posidonia angustifolia* | Sediment instability (blow outs) | Sergeev et al. (1988) |
| _____–1949 | Gulf St Vincent | 900 | *Heterozostera tasmanica; Posidonia sinuosa; Amphibolis antarctica* | Coastal construction (retaining walls, groynes), sediment burial | Shepherd et al. (1989) |
| *Tasmania* | | | | | |
| 1948–1990 | Birch Point | 397 | *Species?* | – | Hamdorf and Kirkman (1995) |
| 1948–1990 | Ralphs Bay | 430 | *Zostera muelleri, Heterozostera tasmanica, Halophila australis* | – | Hamdorf and Kirkman (1995) |

(continued)

**Table 20.1** (continued)

| Timeframe | Location | Area of loss (ha)[a] | Species | Drivers of loss | Reference |
|---|---|---|---|---|---|
| 1948–1990 | Pittwater | 1,201 | *Zostera muelleri, Heterozostera tasmanica*[b], *Halophila australis* | – | Hamdorf and Kirkman (1995) |
| 1970–1990 | Norfolk Bay | 2,140 | *Zostera muelleri, Heterozostera tasmanica*[b], *Halophila australis* | – | Hamdorf and Kirkman (1995) |
|  | Clarence River | 445 |  | – | Hamdorf and Kirkman (1995) |
| *Victoria* |  |  |  |  |  |
| –1983 | Western Port | 17,800 | *Heterozostera tasmanica*[b], *Zostera muelleri* | Sedimentation of fine muds | Bulthuis (1983) |
| *Western Australia* |  |  |  |  |  |
| 1941–1992 | Rottnest Island | 46 | *Posidonia sinuosa, Posidonia australis* | Mooring damage-erosion | Hastings et al. (1995) |
| 1953–2002 | Warnbro Sound | 73 | *Posidonia australis* | Sediment movement | Bridgwood (2006) |
| 1956–2001 | Esperance Bay | 132 | *Posidonia australis* | Port and coastal construction | Hegge and Kendrick (2005) |
| –1986 | Cockburn Sound | 2,268 | *Posidonia sinuosa, Posidonia australis* | Light reduction Increased epiphytism | Kendrick et al. (2002), Cambridge and McComb (1984) |
| –1986 | Princess Royal Harbour | 810 | *Posidonia australis, Amphibolis antarctica* | Light reduction Increased epiphytism (eutrophication) | Bastyan (1986) |
| –1986 | Oyster Harbour | 720 | *Posidonia australis, Amphibolis antarctica* | Light reduction Increased epiphytism (eutrophication) | Bastyan (1986) |
| 2011–2014 | Shark Bay | 100,000[c] | *Amphibolis antarctica* | Thermal stress combined with light stress | Fraser et al. (2014), Thomson et al. (2015), Arias-Ortiz et al. (2018) |

[a] Represents reported area lost during the timeframe, does not account for recovery and loss during the time frame given, or subsequent recovery or loss

[b] Now recognised as *Zostera muelleri*; for current status of *Heterozostera* see the Appendix

[c] Based on surveys of A. antarctica cover at 100+ sites extrapolated to whole ecosystem. Median of a range from 4 to 80% loss

opportunistic and colonising seagrass species dominate in tropical areas (Kilminster et al. 2015) and due to faster growth rates and large numbers of seeds in the seed bank, they can often exhibit greater resilience to perturbations (Rasheed et al. 2014) compared to persistent species in more temperate zones where recovery rates are slower (Walker and McComb 1992; Irving et al. 2010). The subtropical region of Shark Bay, Western Australia, is at the interface of temperate and tropical marine ecosystems, and thus supports high biodiversity, including 12 seagrass species (Walker et al. 1988; Kendrick et al. 2012a, b). An abnormal marine heat wave event in the summer of 2011 combined with extreme cyclonic flooding (Fraser et al. 2014; Thomson et al. 2015) caused up to 100,000 ha based on Arias-Ortiz et al. (2018) loss of the temperate seagrass *Amphibolis antarctica*. Seagrass losses in temperate zones are generally a result of human activities, rather than natural events, such as cyclones (Table 20.1), although winter storms can be damaging.

## 20.2 Major Loss Mechanisms of Decline

The main factors regulating the colonisation, growth and health of seagrasses are light, substrate and wave exposure (Table 20.2), but the presence and distribution of seagrasses at different localities are also regulated by a number of other site specific physical, chemical and biological factors (Table 20.2). Activities or events that cause physical, chemical and biological change to the environment and impede seagrass growth and health (Table 20.2) are likely to result in a specific state change to the seagrass meadow (manifested as a change in, for example, depth limit, species composition, standing crop, total loss or fragmentation). Seagrasses are able to resist, adapt and/or recover, in some instances, to either a similar pre-disturbance stable state, or in other instances another species may come to dominate (see Chap. 9), thus an alternative ecosystem may come to dominate.

### *20.2.1 Anthropogenic Pressures*

A recent study of sediment archives through core sampling in a *Posidonia australis* meadow in Oyster Harbour, Western Australia, has provided a record of ecosystem dynamics and processes over the last 600 years, pre- and post-European arrival (Serrano et al. 2016). Two distinct environmental degradation phases were identified; the first one (1850s–1950s) followed the onset of European settlement in Australia and was characterized by a large increase in sediment accumulation rates and fine-grained particles, driven primarily by enhanced run-off due to land clearing

**Table 20.2** The main environmental factors regulating growth, distribution and health of seagrass

| Factor | Processes influenced | Observed changes to seagrass plant morphology, and meadow extent and configuration[a] |
|---|---|---|
| Light | Photosynthesis | Lower depth limits; growth rates; shoot density |
| Hydrology (i.e. currents, wave action and tide) | Seagrass-sediment feedback | Upper depth limits; vegetative (rhizome) spreading; seedling colonisation; accumulation of fine sediments and organic matter; shoot density; direct influence on associated biota; meadow configuration (pattern, shape and juxtaposition of patches) |
| | Epiphytic biomass growth | |
| | Sediment grain size and associated nutrient and oxygen exchange | |
| | Turbidity (see light) | |
| | Desiccation (tidal exposure) | |
| | Diffusion of nutrients/gases across leaf boundary layers | |
| | Erosional/depositional processes | |
| Geology | Erosional/depositional processes as well as the availability of nutrients and phyto-toxins | Growth, morphology and landscape configuration of seagrasses |
| Temperature | Plant metabolic rates (seagrass and associated algae) | Growth rates and distribution |
| | Flowering, germination | |
| | Desiccation | |
| Oxygen | Aerobic metabolism | If oxygen supply to meristems and roots of the seagrass is inhibited for long periods of time the plant risks reduced growth rates or mortality |
| Salinity | Osmoregulation | Biogeographical distribution |
| Nutrients (C, N, P) | Photosynthesis, growth, light availability | Epiphyte cover, seagrass density |

for agriculture in the catchment. The second (1960s until present) was identified by a sharp increase in phosphorus concentration and the increasing contribution of algae and terrestrial inputs into the sedimentary organic matter. This provides compelling evidence of the documented eutrophication through human-derived activities in the Oyster Harbour catchment area and the subsequent extensive loss (80% or a total of 720 ha) of seagrass meadows.

Duarte (2002) defined two categories of anthropogenic pressures on seagrasses. Firstly, direct proximal pressures which affect seagrass meadows locally and secondly, indirect pressures which have the potential to affect meadows on a larger and even global scale. These have been identified as endogenic managed pressures and exogenic unmanaged pressures (Elliot 2011). Direct impacts (endogenic managed) tend to be on a smaller scale, and include mechanical damage as a result of development in the coastal zone, mobile fishing gear and recreational boating activities, eutrophication, siltation from agriculture, and urban waste and aquaculture (Short and Wyllie-Echeverria 1996). Indirect pressures (exogenic unmanaged) include climate-driven changes, changes in global sea levels, increases in ocean temperatures, $CO_2$ and UV radiation, regional nutrient enrichment or eutrophication, as well as over-harvesting of apex predators leading to top down effects on oceanic food webs. These indirect impacts have the potential to be devastating to seagrass habitats, but due to the scale of the problem, are often difficult to control. The loss of seagrass is reversible in some cases, through either natural recovery or active intervention via restoration. Land reclamation activities, such as those for ports, lead to a permanent loss (Grech et al. 2011; Coles et al. 2015).

Nutrient enrichment has been responsible for major losses of seagrass across Australia, specifically adjacent to large urban areas (Morris et al. 2007), or where rivers drain large catchments which have been intensively farmed. Localised losses have been linked to sewage outfalls, agricultural runoff and point source inputs (e.g. from boating and aquaculture industries). Nutrient enrichment has been experimentally linked to increased growth of epiphytic algae (in particular filamentous algae) (Cockburn Sound Study, Anon. 1979; Bryars et al. 2011), drift algae and phytoplankton (refs). Each of these plant algal groups has the potential to compete for nutrients and reduce the amount of light reaching the seagrasses (Ralph et al. 2007; Collier et al. 2012). Excessive nutrient input over ~50 years (1949–2002) due to sewage sludge, wastewater, and industrial outfalls was linked to the loss of over 5,200 ha of *Amphibolis antarctica* and *Posidonia* spp. meadows along the Adelaide Metropolitan coastline, due to excessive overgrowth by epiphytes (Tanner et al. 2014). However, some effect of toxins in the sewage effluent cannot be excluded. Loss of the seagrass exposes the seabed to wave action causing sediment resuspension, which further increases turbidity, thereby creating a strong positive feedback loop of eutrophication, impeding any autogenic recovery (Folmer et al. 2012). This then resulted in loss of sandy beachfronts and water turbidity that continue to plague the Adelaide coastal areas.

Physical disturbance can occur on both intertidal and subtidal seagrass meadows. It may be caused by trampling, dredging, use of mobile fishing gear, as well as adjacent coastal development, such as sea walls and groynes, which can alter natural hydrodynamic processes that require costly solutions resulting in environmental problems (e.g. Oldham et al. 2010). Intensive boat activity may result in direct physical damage to the seagrass meadows by propeller, anchor or mooring

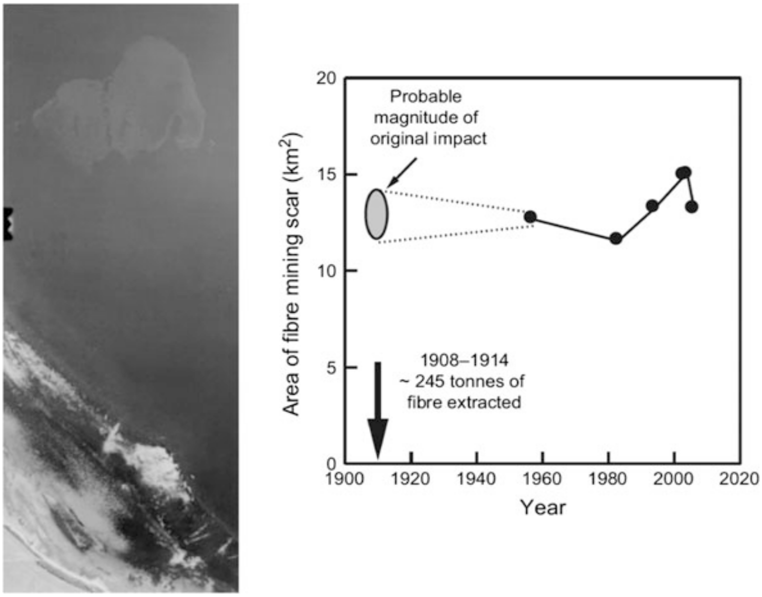


**Fig. 20.2** Sand scar caused by fibre harvesting of seagrass (top of left image) and the evidence for lack of recovery over the last century (right) (reproduced from Irving 2013)

scar, or hull grounding during shore landings. Scars often dissect a seagrass meadow channelling water currents which inhibit recovery (Cole 2012). Such physical disturbances may leave an enduring and unwanted legacy. Seagrass fibre harvesting in South Australia in 1908 produced 1,200 ha sand scars that show little to no evidence of autogenic recovery more than a century later, despite being located on an otherwise pristine coastline (Irving 2013; Fig. 20.2). The creation of a novel habitat by the original disturbance now appears wholly unsuitable for seagrass colonization and persistence.

### 20.2.2 Natural Pressures

Some of the largest and most acute losses of seagrass have been the result of natural catastrophic events. In addition to the aftermath of Cyclone Sandy (see Table 20.1), the resulting high turbidity from the flooding of the Mary and Burrum Rivers and another cyclone Cyclone Fran resulted in the loss of an estimated 100,000 ha of seagrass in Hervey Bay (NSW) in 1993 (Preen et al. 1995). Catastrophic events are not limited to the tropics, for example a series of abnormally low tides coincided with high summer temperatures and dry winds caused the die-back of ~11,000 ha of intertidal seagrass in Spencer Gulf, South Australia (Seddon et al. 2000). Whilst recovery from a single catastrophic event may be possible, if such events become more frequent, recovery may be hampered. For example, there is evidence that a succession of La Niña type weather events (above average rainfall and severe storm and cyclone activity) resulted in a decline in seagrass cover across the Great Barrier Reef World Heritage Area (Coles et al. 2015; McKenna et al. 2015). A more recent ecosystem-wide loss occurred from large-scale defoliation of *Amphibolis antarctica* in the Shark Bay World Heritage Area during an abnormal marine heat wave in 2011 that drove water temperatures up to 4 °C higher than average summer temperatures, combined with extreme cyclonic flooding (Fraser et al. 2014). The seagrass meadows did not recover over 3 years, and the resultant increase in detrital carbon in the system resulted in further loss (Fraser et al. 2014; Thomson et al. 2015) that had ecosystem-wide impacts (Thomson et al. 2015). There is approximately 3,700 km$^2$ of *A. antarctica* in Shark Bay (Walker et al. 1988) and long term monitoring of sites across the bay reported between 60–80% permanent loss of cover from the 2011 marine heat wave, suggesting the loss could be as great as 1, 000 km$^2$ (100,000 ha). Presently the Western Australian Department of Parks and Wildlife are determining a more accurate overall loss of *A. antarctica* using remote sensing.

## 20.3 Seagrass Loss Versus Restoration

Globally, an estimated 33,000 km$^2$ of seagrass has been lost since 1879 (Waycott et al. 2009), with much of this loss directly impacting local economics (e.g. fisheries and tourism) and traditional ecosystem services arising from seagrass meadows. Australian coastlines have followed suit, with quantified totals of ca. 267,000 ha (including seagrass loss in Shark Bay, Thomson et al. 2015). Yet, despite large numbers of restoration studies (Fig. 20.3) and decades of restoration practice across Australia (and around the globe), our understanding of the ecological mechanisms underlying successful and unsuccessful seagrass restoration is not keeping pace with the rates of loss (van Katwijk et al. 2016) and societal needs for restoration (Abelson et al. 2016). Successful restoration has been rare and almost always at a scale orders of magnitude lower than the scale of loss. For example, successful seagrass restoration programs, which include both active (replanting) and passive (restoring or removing disturbance regimes) approaches in Australia have been on the scale of <10’s ha (active, Bastyan and Cambridge 2008; Irving et al. 2010, 2014; Tanner et al. 2014) and 10’s–100’s ha (passive, Bryars and Neverauskas 2004) of area revegetated. Indeed, returning degraded seagrass ecosystems to any semblance of their former extent and diversity will require many orders of magnitude more of restoration effort, in terms of science (restoration ecology) and practice (ecological restoration) and their interactions (see McDonald et al. 2016) just to prevent further seagrass loss (Irving et al. 2013; Abelson et al. 2016).

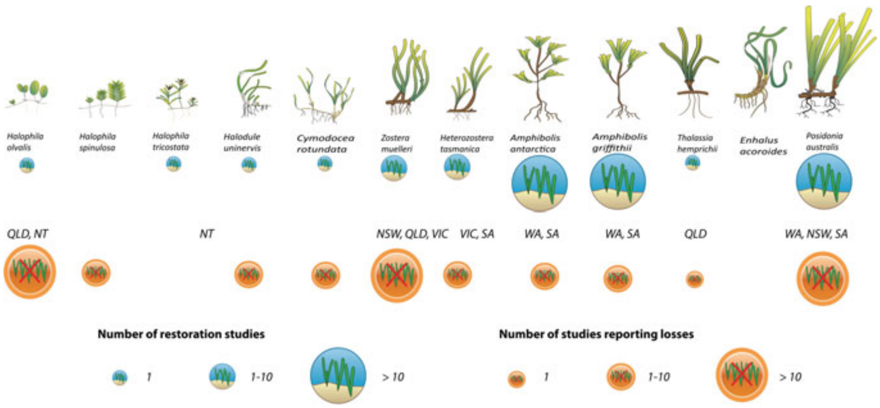
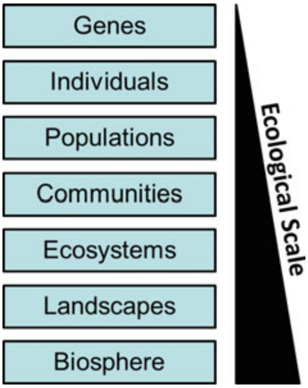


**Fig. 20.3** Diagrammatic representation of number of studies reporting losses and restoration for seagrass species in Australia

## 20.4 Restoration Ecology of Seagrasses

The science of seagrass restoration (restoration ecology) is complex, and though still a young science, has strong foundations built from several decades of ecological research. The conceptualisation of ecological processes has improved our understanding of how these processes interact among many linked components and across temporal and spatial scales spanning several orders of magnitude (Fig. 20.4). It is this level of understanding that is integral to successful restoration practices. Clearly, none of these components are independent, and yet to advance restoration ecology and indeed its practice (ecological restoration), we need to understand both within and cross-scale processes in a strategic and systematic manner.

**Fig. 20.4** Conceptualisation of life in terms of scales and hierarchies of biological organisation



There is a diverse body of theory addressing many aspects of ecological interactions in seagrasses (summarized in Larkum et al. 1989; Hemminga and Duarte 2000; Larkum et al. 2006; this book, Chaps. 7–10). This is highly relevant to both the science of restoration ecology and the practice of ecological restoration. In the following sections, we provide examples of the links between ecological theory (within each level of organisation) and the science of seagrass restoration ecology, and where possible include future research directions.

### *20.4.1 Genes*

The application of genetic principles for restoration ecology has been well-studied in terrestrial systems (e.g. Bozzano et al. 2014), but less so in the marine environment. Research suggests that it is important to use locally-adapted material (vegetative cuttings, seeds), and this is widely recognised by practitioners and restoration geneticists as '*best-practice*' and routinely incorporated as one of the many tools available for ecosystem restoration (Vande Mijnsbrugge et al. 2010; Kettenring et al. 2014). Genetic composition also needs to be considered when sourcing material for restoration, in recognition that species are spatially and genetically structured (Kettenring et al. 2014). Genetic diversity varies widely within seagrass meadows, from large almost single clone meadows to extremely high levels of clonal diversity (e.g. Evans et al. 2014; Sinclair et al. 2014; Hernawan et al. 2017).

Four major genetic issues require consideration when sourcing biological material for restoration, regardless of whether sourcing transplant material or seeds. The issues include (1) adequate genetic diversity for the resilience of restored populations in relation to environmental variation and change, (2) use of locally-adapted material where possible to ensure it is best suited to local conditions (local genetic provenance), (3) source and restored meadows contain a sufficient number of unrelated individuals to avoid inbreeding depression (ensure seed production in outcrossed species), (4) structural gene complexes that provide local adaptation are preserved to avoid loss of fitness through breakdown in future generations (outbreeding depression) (Frankham et al. 2011; Weeks et al. 2011).

A retrospective investigation of genetic diversity within a small successfully restored *Posidonia australis* meadow in Cockburn Sound, Western Australia, indicated that high genetic diversity in the donor site (approximately 16 km north of the restoration site) was captured in the restored meadow (Sinclair et al. 2013). The success of this small scale restoration effort could not directly be attributed to genetic diversity alone. However, a healthy, now reproducing, meadow has been established within a decade, with active recruitment from seeds occurring both within the transplant area and around it (Fig. 20.5). This suggests that once some transplants become established, the seafloor may stabilise enough to allow natural recruitment from dispersing seeds within or from other meadows, or the plants provide a natural trap for seeds to settle and establish.

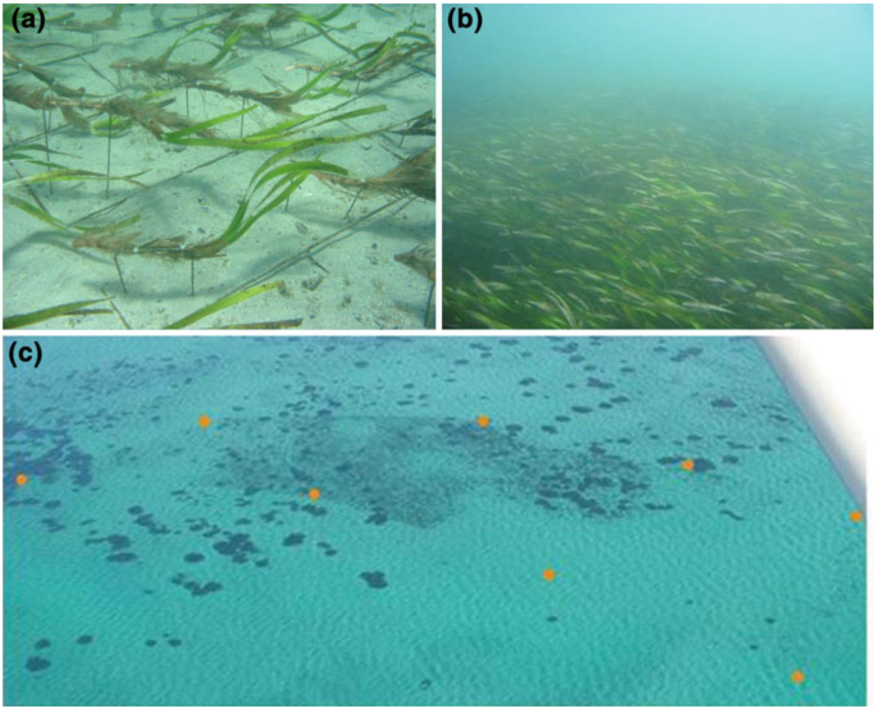


**Fig. 20.5** *Posidonia australis* restoration site in Cockburn Sound, Western Australia. **a** Transplants in situ, prior to the pegs being covered with sediment (2007); **b** high shoot density in the established transplanted meadow (2011); **c** aerial view of the restoration site (within yellow markers) showing improving shoot density from the transplants as well as natural recruitment occurring from vegetative regrowth and new seedling recruits. Photos courtesy of Jennifer Verduin

'Home-site advantage' implies the use of locally-adapted genotypes will typically lead to better restoration outcomes when compared to non-local genotypes (Hufford and Mazer 2003). However, this is not always the case (e.g. Jones 2013) and may be particularly relevant to marine ecosystems. Local provenance genotypes may be a poor match when the restoration site conditions are highly modified, such as through changes in hydrology, sediment type and heavy metal contamination, as is observed in many degraded marine systems. Selective sourcing of plant material through composite, admixture, or predictive sourcing (Broadhurst et al. 2008; Breed et al. 2013) may provide alternative strategies to maximize evolutionary potential and restoration success of degraded sites. In addition to localised changes as a result of anthropogenic activities, the oceans are undergoing substantial changes, in particular, a general warming or tropicalisation of temperate marine ecosystems (Vergés et al. 2014; Hyndes et al. 2016), ocean acidification (Koch et al. 2013), and increasing frequency and intensity of extreme events e.g. marine heat waves (Fraser et al. 2014; Thomson et al. 2015) and flood events. The response of marine organisms to these changes is not well-understood, although systems will be directly or indirectly affected on a much wider scale than an individual restoration site. Increasing our knowledge of the physiological and genomic responses of species to changes in temperature, light, salinity, and pH will help improve predictions for future ecosystems in terms of shifting ranges, extinctions, and how restoration efforts can target specific problems.

The development of Next Generation Sequencing methods (NGS) allow much larger parts of the genome to be explored, as well as linking gene regions to functional traits through gene expression (Allendorf et al. 2010; Williams et al. 2014). Changes in gene expression levels of candidate genes in marine plants are putatively relevant to areas such as thermal and salinity tolerance, light regimes, and ocean acidification (e.g. Franssen et al. 2014; Lauritano et al. 2015). Approaching seagrass restoration from a genomics perspective will provide insight into how plants can respond to changing climatic conditions and how we go about building resilience into ecosystem restoration. However, the current rate of climate change is rapid, and evidence is accumulating that both genetic and ecological constraints may limit the ability of populations to adapt to large-scale rapid climate change. Such constraints may predispose species to respond through range shifts and phenotypic plasticity, rather than through evolutionary adaptation (Jump and Penuelas 2005; Merila 2012). These new technologies could provide substantial 'future-proofing' power, if incorporated into an adaptive management approach. Local genetic adaptations will be increasingly weakened in situ as the climate changes, so a static view of genetic-environmental relationships will no longer be relevant (Prober et al. 2015). The impact of environmental changes can be examined through genetic monitoring of adaptive responses via repeated analysis of the same populations over time, distinguishing between phenotypic and molecular genetics approaches (Hansen et al. 2012). Restoring resilient seagrass meadows requires an understanding of genomic diversity and adaptation, and experimental testing of short-term plastic responses (phenotypic) versus genetic adaptation (generation to generation) under different environmental conditions. This has the potential to improve resilience in ecosystem restoration through climate-adjusted provenancing (Prober et al. 2015), in combination with practical solutions to scale-up marine restoration areas (Gillies et al. 2015).

The assembly and characterization of two seagrass genomes have recently been completed using Next Generation Sequencing technologies: one northern hemisphere species *Zostera marina* (Olsen et al. 2016), and one southern hemisphere species *Zostera muelleri* (Lee et al. 2016) in which a genome-wide survey has also been done (Golicz et al. 2015). However, traditional genetic diversity metrics, such as allelic diversity, genotypic/clonal diversity and gene flow estimates obtained from microsatellite DNA markers, are still valuable tools for current restoration and mitigation activities (Jahnke et al. 2015). Microsatellite DNA markers have recently been generated for a number of Australian seagrass species, so it is expected that substantial data collection will continue. Few marine restoration projects have considered the choice of donor site when sourcing material for restoration, in terms of the source location relative to the restoration site and the amount of genetic diversity, with only one recent study citing restoration failure due to genetic issues (Jahnke et al. 2015). The collection of genetic data for a much wider range of Australian species will allow marine restoration actions to consider genetic issues. These data are expected to provide important information on genetic diversity and gene flow in these species and provide valuable additions to restoration programs.

### *20.4.2 Individuals*

Many examples of failed seagrass restoration can probably be attributed to a casual consideration of the basic physiological requirements of adequate sunlight for photosynthesis, nutrients for growth, and sediment in which to anchor. Seagrasses are most often transplanted from ‘healthy donor meadows’ to unsuitable habitat or degraded environments from which meadows have been lost due to declines in water or sediment quality. Consequently, transplanted individuals are often exposed to significant and sudden changes in environmental conditions, including reduced light intensity (often due to turbidity caused by silt and phytoplankton blooms), excessive sedimentation, eutrophication from terrestrial sources, and more mobile sediments and water currents (Orth et al. 2006). Any or all of these factors can cause rapid restoration failure. For example, seagrass transplant failure on Australia’s more hydrodynamically-active southern coastline have frequently been caused by excessive erosion of surrounding sediments (van Keulen et al. 2003; Irving et al. 2010), change in hydrodynamics of mooring scars (Hovey et al. unpublished data), or very slow rates of recovery of blast scars within *P. australis* meadows at Jervis Bay (Meehan and West 2000). Recent evidence shows eutrophication causes reduced leaf turnover rates and leaf loss due primarily to the overgrowth of leaves by epiphytes (Irving, unpublished data). In addition, supplemental inorganic nutrient additions to sediments of species with inherently slow growth rates may be of limited benefit to plant performance. For example, addition of nitrogen and phosphorus fertilizers to marine sediments of *P. australis* both in situ (adult transplants) and ex situ (seedlings) resulted in a relatively minor positive effect on above-ground growth, but significant reductions in root development and therefore anchorage potential (Cambridge and Kendrick 2009; Hovey et al. 2011; Statton et al. 2013). Seagrasses may be able to adapt to novel (or altered) environments in time however it is highly unlikely that transplants can rapidly adapt to such suboptimal conditions.

Most seagrasses can readily absorb and transport essential resources for survival among connected ramets, which can sustain shoots in sub-optimal conditions and potentially provide a distinct advantage for restoration over isolated plants (e.g. most terrestrial systems). Even so, seagrass transplant trials have often resulted in the complete (or near-complete) loss of transplanted individuals (Paling et al. 2003;

Irving et al. 2010), indicating this clonal advantage doesn't necessarily confer resilience to other stressors. In situations where seagrasses have been transplanted only a few metres from an established, thriving meadow, presumably where macro-environmental conditions are near-identical to their point of origin, transplants often have not persisted (Irving et al. 2010). Key mechanisms driving such loss likely relate to 'transplant shock', involving physical damage to the seagrass roots/rhizome, exhaustion of limited nutrient supplies in the rhizome during establishment, and though largely untested, a disruption/change of sediment micro-environments, such as physical structure (e.g. grain size and porosity), chemistry (e.g. oxic versus anoxic layering), and biology (e.g. infauna and seagrass-associated microbes). Notably, restoration via transplantation appears more successful (on a per unit basis) when larger units (i.e. $\sim 1$ $m^2$) are used, presumably because the centre of the transplant experiences less 'shock', and is thus more capable of establishment in a new environment, than the physically damaged edges of the transplanted unit (van Keulen et al. 2003). However, such transplant units have greater logistical difficulties and require large amounts of effort, extensive damage to existing donor meadows, and costs per transplant unit. An intriguing study with marsh plants showed higher success rates when individual plants were closely rather than sparsely spaced (Silliman et al. 2015). The authors suggested this facilitation was a result of reducing stress and reduced edge erosion. Such a configuration could easily be employed in seagrass restoration projects.

Facilitating natural recruitment can be successfully developed for some species through the exploitation of key biological traits. For example, *Amphibolis antarctica* produce viviparous seedlings with a 'grappling hook' at their base that naturally entangles with shoots and exposed rhizomes of adult meadows, but can be exploited using fibrous hessian bags on the sea floor to intercept seedlings and facilitate their establishment into otherwise bare sand (Wear et al. 2010; Irving et al. 2014). Critically, facilitated patches can expand beyond the original boundary of the hessian bag, and even coalesce into larger meadows (Tanner 2015).

Greater thought needs to be given to building resilience in restored seagrass meadows as we build capacity to restore seagrass, particularly because of the rapid pace of climate change. Such considerations are especially prudent given the relatively large cost of time, resources, and funds that typically support a seagrass restoration project. Physiological evidence shows that seagrasses will benefit from elevated $CO_2$ concentrations (Burnell et al. 2014; Borum et al. 2016), but concomitant impacts of changing ocean climates may indirectly negate such benefits (e.g. ocean warming and acidification can trigger over-grazing of seagrasses by urchins: Burnell et al. 2013).

A question that should be asked is whether restoring a more robust species, or more resilient genotypes is more effective over the long term? Such strategies have been adopted in terrestrial environments, for example, the use of non-local highly salt tolerant species (halophytes) to lower soil salinity for restoration of less tolerant local native species (ref). The cascading effects of changing the identity of such a foundation species on associated taxa, food webs, carbon and nutrient cycles, and sediment stabilization, are generally unknown, but it may be argued that any seagrass, even if a different species than what was originally present, is better than none. However, this decision must be based on scientific evidence to show that an alternate species is the only course of action.

### *20.4.3 Populations*

Local populations may expand by restoring or removing perturbations and disturbance regimes in sites that are only moderately degraded (Bryars and Neverauskas 2004). Such passive revegetation approaches to restoration ultimately rely on recruitment from seed banks (dormant seeds stored within the sediment), seed dispersal from neighbouring populations and/or recruitment of dispersing vegetative fragments (see Chap. 8 for more details on dispersing propagules). The immediate goal of delivering propagules to a site is to establish viable, self-sustaining populations. Success can be measured in several ways (e.g. survival, growth, fecundity) however, assessing the future viability of restored populations does require long-term monitoring and/or demographic modelling, particularly in the long-lived, slow-growing species. Typically, seagrass restoration projects are short-lived and heavily driven by government regulators and commercial agendas. These limit our ability to effectively advance seagrass restoration through restoration ecology principles that include large spatial scale restoration programs (e.g. van Katwijk et al. 2016), long term monitoring of success (Statton et al. 2012), detailed process-based studies on the genetics, physiology and recruitment ecology of natural and restored seagrass meadows and measurement of return of ecological structure and function as well as environmental services (Abelson et al. 2016).

Evaluating the success of a range of life cycle processes, such as seed germination, seedling emergence, transplant and seedling recruitment, growth and reproduction (Fig. 20.6) are the first steps towards optimizing seagrass restoration programs. Seeds and seedlings (direct-developing and viviparous species) have so far been under-utilized in many restoration projects (Statton et al. 2012; van Katwijk et al. 2016) which, in part, stems from our limited understanding of restoration-scale approaches for seagrass seed collection, handling, and delivery techniques to restoration sites for the majority of seagrass species. Nonetheless, recent advances in seed-based restoration for one species in the United States (*Zostera marina*, Marion and Orth 2010a, b; Orth et al. 2012) is encouraging and reveals that seeds could have their advantages over vegetative restoration. The seeds of *Z. marina* can be collected in large quantities (millions of seeds), easily transported and stored, and effectively delivered to large degraded areas (10's–100's ha, Orth et al. 2012). The advantages to using seeds for restoration are significant savings in time, effort and costs over the collection of adult plant material, much less impact to existing meadows, and potentially higher levels of genetic variation (outcrossed seeds will have many different genotypes as compared with plant material potentially collected from a few clones). However, the compromise is that relatively fewer seeds survive, germinate and establish compared to the higher rates of survival with transplants. Newly established seedlings generally have poorly developed roots and rhizomes and thus are more easily washed out by even moderate waves and currents. Marion and Orth (2012) found that significant loss of even deeply buried seedlings occurred in winter when storms are generally more intense. Seed germination and seedling emergence are vital first steps to assess demographic success of seed-based restoration in species that produce dormant seeds (e.g. *Zostera* spp., *Halophila* spp., *Halodule* sp., Fig. 20.6a). For genera that produce direct-developing seeds, such as *Posidonia* and *Thalassia*, survival in the early life-stages can be based on the change in utilisation of maternally-derived reserves (Hocking et al. 1981; Kirkman and Kuo 1996; Kaldy and Dunton 1999; Statton et al. 2012; Fig. 20.6b). Seedling attachment to an appropriate substrate appears to be a critical life stage for viviparous species (*Amphibolis* spp.) prior to seedling establishment (Rivers et al. 2011; Wear et al. 2010; Irving et al. 2014; Fig. 20.6c). Frequent monitoring after seeding is needed to observe these early life-history stages and transitions, and will be particularly important when alternative management strategies are applied which aim to enhance vital rates, such as seedling emergence or subsequent seedling survival (Marion and Orth 2012; Irving et al. 2010; Statton et al. 2017).

Adult plants often have better success per individual than seeds in restoration projects and hence have been the propagule of choice over the past decades (Statton et al. 2012; van Katwijk et al. 2016). These individual plants are typically monitored over time (Statton et al. 2012). The most common vital rate measured is transplant survival with monitoring intensity ranging from frequent (monthly) to infrequent (annually) (Statton et al. 2012). Individual plant survival is not the only measure of initial seagrass transplant success. Individual plant growth rather than survival could be a more practical indicator of the appropriateness of a site for reintroducing plants. For example, *Amphibolis antarctica* can show exceptionally

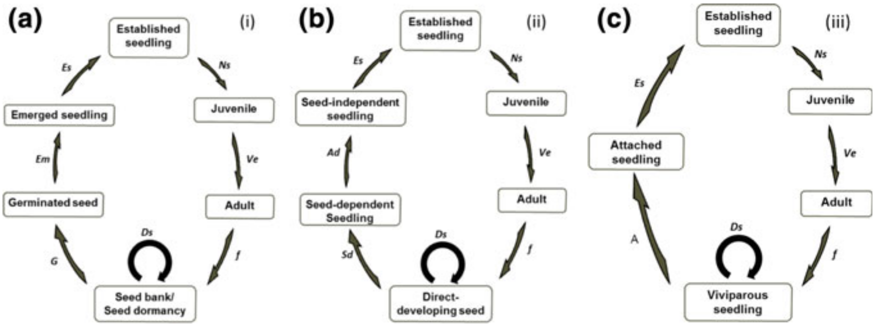


**Fig. 20.6** Life-cycle models describing the demographic stages (boxes) and transitions (arrows) **a** dormant seed, **b** direct-developing seed, and **c** viviparous seedling producing species follow to adulthood. The text describes the developmental stages used to define each transition. Symbols define the transitions; G germination, Em emergence, Es establishment, Sd seed-dependency, Ad autonomous development, A attachment to a substrate, Ns new shoot development, Ve vegetative expansion, f size dependent fecundity, and Ds dispersal of sexual propagules

high numbers of seedling recruitment (>1,500 seedlings $m^{-2}$), but thin to adult densities of ~20 individuals $m^{-2}$ within 12 months (Irving et al. 2014). Notably, these adults persist and exhibit sustained growth over time (at least 4 years post-recruitment; Tanner 2015), suggesting that growth, in the short term, is a more useful indicator of restoration success than individual survival.

A critical benchmark in establishing new populations is the ability to complete the life-cycle. There have been a few successful restoration projects that have observed and reported flowering and fruiting in restoration sites either in Australia (Bastyan and Cambridge 2008; Sinclair et al. 2013) or elsewhere (Piazzi et al. 1998; Orth et al. 2012). However, monitoring reproduction success is a key element to determining the long term success and development of self-sustaining restored sites (Miller et al. 2017). Studies that have quantified reproductive success in seagrasses (e.g. seed output per plant) are rare (Harwell and Rhode 2007; Orth et al. 2012).

Seagrasses do, however, reproduce clonally, ramifying across the seafloor. So the ability of seeds, seedlings or adult transplants to grow and spread clonally is an important indicator of demographic success, particularly if flowering and fruiting of natural local populations is also low. Such spreading may require considerable patience for slower-growing ‘climax’ species. For example, restored patches of *Amphibolis antarctica* in South Australia have taken ~7–10 years to spread from seedlings beyond the boundary of their initial recruitment area and begin to coalesce as adult meadows (J. Tanner unpublished data). Individual survival and growth (see above) are good practical measures of transplant success initially, they become difficult to monitor when plants begin to coalesce. Monitoring shoot density and demography (Marbà et al. 1996) can provide more accurate assessments of meadow performance. Importantly, for a restored population these assessment techniques will allow a better indication of recovery relative to a reference meadow.

Dispersal is a critical attribute for seagrass populations (Kendrick et al. 2012a, b, 2017) and meta-populations (see section on seascapes below), particularly to maintain connectivity (gene exchange, source of new recruits) between restored and natural populations. While active reintroduction of plants (seeds, adults) is one approach to overcome dispersal limitation within a site, it is not feasible to artificially maintain such dispersal in the long term and defeats the purpose of restoring viable, self-sustaining populations. While dispersal and connectivity is being assessed among natural populations, propagule dispersal within or among our restored populations is yet to be quantified, and needs to be addressed and incorporated into future metrics for restoration success.

Translocated populations offer exciting opportunities for demographic analyses, as background knowledge about starting conditions, such as number of seeds or transplants, timing of introduction and baseline environmental characteristics may be more well-known than for natural populations. Most seagrass restoration programs measure success as persistence of plants over short periods of time. However, one area of interest to seagrass restoration ecologists would be to forecast persistence. Population viability analyses could provide valuable foresight on the future success of introductions by projecting future population sizes, stage structures, population growth rates and extinction probabilities (Menges 2000). More recently in restoration, determining the sensitivity of restored population growth rates to particular life-history stages and partitioning these in response to ecological conditions (James et al. 2011; Statton et al. 2017) could potentially advance progress in our understanding of which life-history stage and ecological process is limiting seagrass population growth and persistence. However, these analyses typically require longer-term monitoring of vital rates such as survival, growth, fecundity, recruitment and dispersal. Quantitative information on these rates is poorly understood for natural populations of most Australian seagrass species, let alone for restored populations, though it promises to be a worthwhile and fruitful research direction.

### *20.4.4 Communities*

Transplant units, whether they are seeds, seedlings or adult plants, must pass through a number of biotic and abiotic filters in order to successfully establish. These filters may be considered either top down or bottom up filters that result from interactions among the elements of the community where restoration efforts are undertaken and can be both positive and negative. Transplants, especially seedlings, may be more susceptible to water clarity issues or overgrowth by macro-algae, which can be ameliorated by meso-grazers, which indirectly have a positive effect on the health of a plant by keeping leaf blades free of epiphytes (Orth and van Montfrans 1984; Duffy 2006).

Manipulated bottom-up influences, such as sediment additions of nutrients, have been shown to have both positive and negative influences on seagrass growth. Inorganic nutrient additions have been shown to enhance *Z. marina*, in both naturally occurring (Orth 1977) and transplanted meadows (Orth and Moore 1982), but have little positive influence on *Posidonia* spp. (Cambridge and Kendrick 2009; Hovey et al. 2011; Statton et al. 2012). Nutrient additions also occur via a top down indirect interaction from organisms that live as infauna in seagrass meadows. In particular, bivalves at high densities have a positive influence on *Thalassia testudinum* growth through their biodeposits that are rich in nitrogen and phosphorus and may also have a secondary effect in stimulating nitrogen fixation (Peterson and Heck 2001). The *T. testudinum* plants in return provide protection from predation for these bivalves. This mutualistic relationship was also seen between seagrass, Lucinid bivalves and their sulphide-oxidizing gill bacteria showing enhanced seagrass growth in the presence of these Lucinid bivalves (Van der Heide et al. 2011). This suggests that for restoration efforts to be successful in regions with these bivalves, translocation of bivalves may be important in facilitating restoration success.

Bioturbators could also act negatively on transplants by uprooting or burying them with sediment (Valdemarsen et al. 2011), and both positively or negatively on seeds by burying them both at required depths to germinate or too deep for a germinating seedling to reach the sediment surface (Delefosse and Kristensen 2012;

Blackburn and Orth 2013). Some infaunal species create sediment surface features (pits, burrows, mounds, ripples) that facilitate seed retention and rapid burial by shielding seeds from flow (Orth et al. 1994; Blackburn and Orth 2013). Large grazers, such as fish and urchins, can graze on newly planted leaves requiring projects to provide protection for plants from these grazers or an understanding of where these grazers are likely to be abundant (Statton et al. 2015). Hydrodynamic factors (waves, currents) may act differentially on shallow buried seedlings than a well-established adult plant which may require innovative techniques (e.g. large rocks, C. Pickerell personal communication) or different substratum type (Balestri and Lardicci 2008) to anchor seedlings in these types of environments.

Plant-plant interactions have generally not been considered as important in seagrass restoration projects, but recent studies suggest otherwise. Marion and Orth (2010b) found *Zostera marina* seeds broadcast into *Ruppia maritima* meadows established less successfully than seeds placed on bare sand, unless they were buried. They hypothesized that seed predators in *Ruppia maritima* consumed seeds on the sediment surface before they could be buried. Marion and Orth (2010a, b) found protecting seeds from predators by planting in protective containers increased establishment rates and delaying seed placement until seed predator densities were reduced increased success rates for seedling establishment. Successional approaches may be readily applied to seagrass restoration where late-successional species depend on environmental modification(s) achieved by early colonizing species (i.e. a facilitation model of succession sensu Connell and Slatyer 1977). On the temperate coast of South Australia, the fast-growing, ephemeral *Halophila* spp. are typically the first colonisers of bare sand and are thought to facilitate later-successional species (*Zostera*, *Amphibolis*, and *Posidonia*) through the stabilisation of mobile sediments and enhanced trapping and retention of propagules (Clarke and Kirkman 1989). Successful restoration of *Amphibolis* on this coastline has primarily involved the artificial stabilization of sediment using sand-filled hessian bags on the sea floor (Fig. 20.7), effectively by-passing the need and time

**Fig. 20.7** Newly-deployed hessian bags on the sea floor (left), and bags opportunistically colonised by *Amphibolis antarctica* seedlings approximately one month after deployment in Adelaide, South Australia. Photo courtesy of Jason Tanner

required for primary colonisers (*Halophila* spp.) to facilitate *Amphibolis* spp. (Irving et al. 2010; Tanner et al. 2014). In terms of restoration of desirable species, negative plant-plant interactions have rarely been reported. However, research has shown that fast growing *Halodule wrightii* can out-compete larger, slower growing *Thalassia testudinum* for below-ground nutrient resources (Fourqurean et al. 1995). In addition, the presence of smaller colonising tropical species are reported to be linked to poorer root development and overall poorer transplant growth of larger species (*Posidonia australis*, Statton et al. unpublished data), suggesting competition and/or other potential antagonistic interaction.

### *20.4.5 Ecosystems*

Ecological restoration is the process of augmenting the recovery of a degraded, damaged, or destroyed ecosystem (SER 2004). In contrast to terrestrial restoration, restoration of seagrass meadows generally involves a single species, and it is assumed that other species naturally inhabiting the seagrasses will re-establish once conditions are suitable. We are compelled to restore seagrasses because of their ecological value and provision of critical ecosystem services (e.g., nutrient cycling, fisheries, carbon storage, seafloor stability, water quality). It is recognized that restoration of ecological processes, such as carbon sequestration (Marbà et al. 2015), return of faunal diversity (McSkimming et al. 2016) or commercially important species (Blandon and zu Ermgassen 2014), may be good performance indicators of seagrass restoration success. Historically, seagrass restoration efforts have focused on single species and populations, with some work on community assemblage. Yet, there has been little focus on the linkage between the reintroduction of seagrass structure and return of ecological function (e.g., biogeochemical processes, trophic dynamics, nursery habitat) and how this can be achieved in a restoration context.

Restoration of marine biodiversity within seagrass dominated ecosystems largely relies on the ability of organisms to naturally recruit via the water column, as is well-demonstrated by the natural recruitment of submarine structures such as piers, artificial reefs and oil rigs (Ajemian et al. 2015). So to some degree, if seagrass meadows (single or multi-species) can be successfully restored, then other marine species will ‘find’ the new habitat, establish and survive long term. One such study found epifaunal richness and total abundance recovered prior to the recovery of seagrass structure, however, full recovery of seagrass was required before the composition and relative abundances of the epifaunal community matched that of the natural seagrass meadow (McSkimming et al. 2016). The problem is when the newly restored habitat is isolated (physically) with low connectivity to existing habitats (beyond the natural dispersing distances of local species) then the trajectory to a fully functioning seagrass ecosystem may be diminished. Restoration of the seagrass will make significant changes to the local environment (improving sediment stability and turbidity), thus making a significant contribution to the process of ecosystem restoration. However, the full set of processes requires much greater biodiversity including the sediment and wrack dwellers (micro-organisms and fauna to facilitate nutrient sourcing, cycling and trophic transfer) (Hyndes and Lavery 2005; Heck et al. 2008). Consideration must also be given to how an ecosystem operated before its decline, in order to ensure a return to full ecosystem functioning post restoration. For example, in terrestrial ecosystems, the restoration of degraded mine sites may require ameliorating soil, transplanting soil microbes, and attracting plant pollinators (Miller et al. 2017).

Genetic diversity can have important ecological consequences at the population, community and ecosystem levels, and in some cases the effects are comparable in magnitude to the effects of species diversity (Hughes et al. 2008). Few data are available to assess the potential ecosystem-level importance of genetic diversity within seagrass species; however, a link between increased genotypic diversity, resistance and resilience has been documented (Hughes and Stachowicz 2004; Hughes et al. 2008). Reynolds et al. (2012) also report a positive impact of genetic diversity in *Zostera marina* along a depth gradient, suggesting that ecosystem restoration will significantly benefit from obtaining sources (transplants or seeds) with high genetic diversity and from restoration techniques that can maintain that genetic diversity.

### 20.4.6 Seascapes

Australian seagrass habitats are part of a larger ecosystem, the seascape, which includes many other functionally important habitats for example mangroves, shell fish reefs, coral reefs and mudflats. There is considerable evidence for the physical, biological and chemical relationships connecting these components of the system (Nagelkerken et al. 2000; Mumby 2006; Moberg and Rönnbäck 2003). Such connectivity often means that the factors resulting in the loss of seagrass may also impair the functioning or cause loss and degradation of adjacent or connected habitats (e.g. Lamb et al. 2017). In fact, the loss of these habitats may be the cause of the loss of seagrass (or vice versa, see Nyström et al. 2012). Despite these wider ecosystem processes, marine restoration efforts currently focus on just one component of the system, where there may be a requirement in some situations to tackle the problem with an ecosystem based restoration approach, whereby multiple habitats are restored to re-establish positive ecosystem interactions (Moberg and Rönnbäck 2003).

Landscape (or seascape) ecology is the study of the relationships between pattern and ecological processes across a mosaic of landscape elements (e.g. habitat cover type or patches) over a range of scales. This includes the influence of spatial patterns due to habitat heterogeneity (structure, matrix, mosaic) and spatial dynamics (population dynamics, environmental change, habitat fragmentation) (see Chaps. 7–10 for further details). As such, a seascape approach has wide applications for seagrass restoration and rehabilitation (Bell et al. 1997), some of which have already been considered in Australian seagrass restoration efforts.

A wide range of questions can be answered by taking a landscape approach to seagrass restoration. One of the first stages in any restoration is the recognition that there has been seagrass decline and that natural recovery is being compromised. Change over time and space within a landscape has been conceptualized by a spectrum of models, all of which model the change (from one cover type to another, for example seagrass to bare substrate) in different landscape elements (patch type, class, cover type) over time (Weinstein and Shugart 1983), Landscape models can be employed to predict the dynamics of the system to identify the need for restoration when long-term data (either continuous or discrete) exist for a location (Seddon et al. 2000). For example, observations at a landscape scale and modelling techniques can examine if a landscape is in a process of fragmentation or accretion, an important consideration in restoration decision making. This assessment may be at the scale of an individual meadow or across a region where meadows and potential seagrass habitat are separated by unsuitable habitat, but are interconnected through the dispersal of propagules (a metapopulation approach). Importantly, any changes over space and time at a landscape scale, need to be recognised within the natural dynamics of the seagrass meadow form (Kilminster et al. 2015). In a review of Australian seagrass complexity for management, Kilminster et al. (2015) identified two main forms of seagrass meadow ‘enduring’ (persistent over time, with small temporal changes in morphometrics) and ‘transitory’ (do not persist over time, with local extirpation and recolonization occurring over annual and longer cycles) depending on the habitat modifiers (i.e. local disturbance regime, for example water depth, wave exposure) and methods of re-establishment (e.g. from seed banks or propagule immigration). Seagrass restoration is often considered to focus on the re-establishment of enduring meadows, however, transitory seagrass meadows (more common in tropical Australia) are also candidates for restoration, where either local extinction or recolonization have been adversely impacted by human activities. Knowledge of metapopulation dynamics are critical to applying restoration approaches for transitory seagrass meadows.

Metapopulations are defined as regional populations of seagrass with asynchronous extirpation of patches, but with migration allowing connectivity among patches (Kritzer and Sale 2004; Bell 2006). Many species of seagrasses have life history traits that fit well with a relaxed definition of metapopulations and the critical components of metapopulation theory (i.e. colonisation, extinction and dispersal). Recent reviews of seagrass movement ecology and dispersal potential (Kendrick et al. 2012a, b; McMahon et al. 2014) combined with knowledge of landscape-scale patch distribution (Kendrick et al. 2008; Ooi et al. 2014) can go some way to providing explanations for the lack of natural recovery in instances where the cause of initial seagrass loss have been removed or ameliorated. The likelihood of a restored seagrass patch receiving propagules from neighbouring patches or even the potential for the active placement of seagrass transplant efforts to improve connectivity between patches increases the probability of metapopulation persistence (Orth et al. 1994; Ruiz-Montoya et al. 2012; Weatherall et al.

2016). An understanding of the spatial organisation of the wider metapopulation within which a restoration plot may be situated, knowledge of the connectivity (immigration and emigration) with other meadows and the mechanisms for natural recolonization or extinction risk may all aid in seagrass restoration decision making and improve the chances of success. Connectivity among eelgrass (*Zostera marina*) populations along the North American Atlantic coast was evaluated among restored and naturally recruited populations (Reynolds et al. 2013). Their results showed that metapopulation dynamics were important to the natural recovery of seagrass ecosystems that have experienced catastrophic loss over large spatial scales. However, natural recovery processes are slow and inefficient at recovering genetic diversity and population structure when recruitment barriers were present, such as a limited seed source.

Knowledge of landscape scale spatial configuration is also useful to identify the need for restoration interventions at a site. There is some evidence that, for seagrasses influenced by wave and current exposure, there is a critical threshold of fragmentation beyond which the contiguity of cover cannot be maintained (proposed as 59% by Fonseca and Bell 1998). If this is the case, the potential exists for landscape modelling and the analysis of spatial patchiness to identify seagrass meadows approaching this threshold and for restoration and rehabilitation to be employed prior to more significant losses. Conversely, there is also likely to be a critical threshold in terms of contiguity of cover which may need to be reached during restoration efforts in order for meadows to persist long-term, although it is likely the two thresholds would differ. Van der Heide et al. (2011) examined system feedbacks and hysteresis following large scale seagrass dieback in the Wadden Sea and identified a critical transition between alternative stable states. They proposed that a lack of success in seagrass restoration worldwide may be due to the small scale of restoration attempts, because small populations were unable to modify their environment enough to shift back to the stable seagrass state. Knowledge of natural local seagrass patch configurations may also aid in monitoring the restoration success as restoration blocks morph into their natural configurations.

Similarly, the spatial analysis of historical seagrass landscape configuration may provide important insights for the layout design and configuration of seagrass transplant units. Australian seagrass restoration studies have identified that when using plug or turf transplants, size of the patch and the distance from other patches is an important consideration. Van Keulen et al. (2003) examined the effect of increasing planting unit size and stabilising sediment and found that survival of *Amphibolis griffithii* improved with increasing plug size. The natural spatial arrangement of seagrass patches are influenced by physical factors, such as hydrodynamics and associated erosion or sedimentation (Inglis 2000), which can manifest in specific spatial patterns. A prominent example here, are the patches of distinct reticulated *Cymodocea nodosa* seagrass, which result from natural subaqueous dune migrations (Marbà and Duarte 1995). Traditionally, seagrass transplants have been planted out in square grid patterns, which, if the seagrass transplants survive often eventually morph into more rounded patches, due to erosive processes and multi-directional growth (Bastyan and Cambridge 2008).

Understanding the factors contributing to natural configuration may allow the optimal design of transplant positioning and choice of donor plants, thus increasing the chances of success. An understanding of landscape patch dynamics could also aid in donor transplant selection within a seagrass landscape, due to observable changes in plant morphology across the seascape. For example, Jensen and Bell (2001) identified that internode length differed significantly within a patch, with longer internodes on the edge compared to the centre of the patch, and on the flood edge of a patch versus ebb edge.

The configuration and cover types in the landscape mosaic within which seagrass restoration is attempted may also influence success in terms of persistence and ecosystem function of restored areas. Van Keulen et al. (2003) examined the effect of stabilising sediment and found that survival of *Posidonia australis* plugs was greater when transplanted into a bed of *Heterozostera* compared with bare sand or a protective mesh border, indicating the importance of the matrix habitat. Analysis of past configurations at a site can identify edaphic gaps/patches—i.e. gaps in vegetation associated with topography or edaphic features such as sediment conditions (Bell et al. 1999), where transplantation should be avoided. The specific configuration of the landscape mosaic, for example the proximity or juxtaposition of other habitats to the seagrass restoration site, may also influence local biotic and abiotic filters to restoration success and therefore success of the seagrass restoration project in terms of the return of function.

The application of seascape theory to seagrass restoration has been limited in Australia, primarily due to a focus on researching appropriate restoration approaches at small scales. However, the initiation of the 'Great Southern Seascapes Program' by The Nature Conservancy to restore temperate habitats including rocky reefs, seagrass meadows, mangrove forests and saltmarshes, may improve success of restoration activities at much larger scales.

### *20.4.7 Biosphere*

Climate change has the potential to significantly influence the practice and outcomes of seagrass restoration by altering the biophysical setting projected for the future. These changes include increases in air and sea temperatures, alterations in the magnitude and seasonality of rainfall, sea level rise, increases in $CO_2$ concentrations, and incidence of extreme climatic events such as marine heat waves, flooding, and storms (Doney et al. 2012). Consequently, developing ecological restoration goals based on a return to reference or pre-disturbance conditions or within the bounds of historical variability may have limited applicability into the future, particularly locations that are vulnerable to a shift in climatic conditions.

Shifts in climatic conditions will introduce novel settings and interactions, leading to a unique set of ecological challenges for seagrasses and for restoration programs. Seagrass restoration practitioners and scientists will need to remain open-minded and innovative in order to overcome these challenges. For example, in

Shark Bay, Western Australia, an extreme marine heatwave in 2011 caused massive losses of *Amphibolis antarctica* meadows (Fraser et al. 2014; Thomson et al. 2015). Similarly, the same extreme conditions appeared to be linked with the changes in reproductive phenology of *P. australis*, such that flowers produced aborted fruit and pseudoviviparous shoots (Sinclair et al. 2016). Coincidentally, in 2011 a restoration program was underway and was impacted by the limited availability of locally sourced seeds and seedlings for these species. Restoration scientists have since begun sourcing and experimenting with seeds from nearby unaffected locations that appeared to be resistant to the extreme conditions (Statton, pers. comms). Another adaptive approach undertaken was to utilize adult plant material from healthy donor populations. The selection of potentially resistant or resilient plant material may be one approach to 'future proof' against climate change.

Climate-driven changes in the distribution of biota are another novel interaction that could profoundly impact seagrass communities and restoration outcomes. Warming ocean currents have enabled a southward range expansion of tropical herbivorous species and increasing their grazing rates in temperate areas (Vergés et al. 2014). For example, warming waters have been associated with large increases in the abundance of parrotfishes into southeastern USA (Fodrie et al. 2010), which consume seagrasses at a faster rate than local native grazers (Prado and Heck 2011). In Australia, the temperate seagrass *Posidonia australis* is generally not heavily grazed by herbivores (White et al. 2011). However, in Shark Bay, Western Australia, *P. australis* grows near its northern limits and is exposed to a broader diversity of herbivores that extend from the tropics. A recent transplantation trial testing the effect of herbivores on *P. australis* transplants found that there was up to 60% daily probability of a transplant being grazed and grazing rates always exceeded daily leaf growth rates (Statton et al. 2015). In addition, even when grazers were offered a selection of seagrass species ranging from the more palatable tropical species (*Halophila ovalis, Halodule uninervis, Cymodocea serrulata*) to less palatable temperate species (*P. australis*, *A. antarctica*), *P. australis* also had a high probability of being grazed, though consumer preference changed across a salinity gradient (Bell, personal observation).

Such examples suggest consideration of climate change impacts be added as a concept of restoration goals. Rather than restoring seagrasses to historic, pre-disturbance conditions, we may improve species persistence into the future by re-calibrating populations to present and future climatic conditions, and promote flexibility to cope with expected variation and uncertainty. The capacity for seagrasses to grow, decline, move, and colonize has enabled species persistence under historical conditions of change. Currently, many human impacts are preventing this capacity including meadow fragmentation, eutrophication and coastal development. With the knowledge that seagrasses have successfully managed change in the past gives rise to new and exciting opportunities for restoration ecologists to 'future proof' seagrasses in overcoming future climate challenges.

## 20.5 Conclusions

Natural and human induced perturbations have resulted in substantial losses of seagrasses across Australia and worldwide. Although loss rates from anthropogenic stressors appear to have slowed since previous estimates, owing in part, to effective protection and conservation measures, as well as greater societal awareness of the value of seagrass meadows, areas already lost have showed little recovery. Indeed, conservation and mitigation of disturbance regimes should always be a first line of defence (Abelson et al. 2016), but ecological restoration is a necessary and more effective management strategy where seagrass habitat is already lost or heavily degraded. However, current global estimates of restoration outcomes reveal that success has been rare and almost always at a scale orders of magnitude lower than the scale of loss. Clearly, many orders of magnitude greater restoration effort, in terms of science and practice is required. Restoration goals, now more than ever, need to reflect increased awareness of the scale of environmental degradation and the recognition that cross-scale, inter-disciplinary approaches are needed to tackle environmental problems (Perring et al. 2015). While restoration has strong scientific underpinnings from ecological theory, it is clear that restoration ecology can also contribute to ecological theory by providing new and novel opportunities to advance our understanding of the mechanisms that promote functional ecosystems.

Whether restoring or removing disturbance regimes, or actively supplying propagules of a single species, these efforts can provide opportunities for controlled, empirical testing of genetic concepts at the population, community or ecosystem level, including local adaptation, selective sourcing of plants to maximize evolutionary potential, and inbreeding and outbreeding depression. Similarly, controlled in situ experimentation within degraded or disturbed systems exposes seagrasses to novel conditions and interactions. Such assessments can reveal the ecophysiological responses of organisms to stress, tolerance of extreme conditions and even aid in determination of seagrass habitat suitability (i.e. bioindicators of change/suitability). At the population level, restoration ecology affords an unparalleled opportunity to assess viability and project the success of restored populations into the future by evaluating and testing predictions about life-cycle processes, such as seed germination, seedling emergence, seedling or transplant recruitment, growth, reproduction and dispersal (sexual and vegetative). Seagrass practitioners have gained knowledge about interactions among the community elements, such as the influence of top down or bottom up processes during restoration efforts. These processes can be both positive and negative, and restoration practices have promoted opportunities to investigate these higher-order processes, including community assembly, trophic dynamics, facilitation, competition and successional pathways. Assessment and evaluation of the functional return and therefore value of restored seagrass meadows has been limited, which for the large part, is owed to the limited number and small scale of successful restoration attempts in Australia and globally. Some attempts have shown return of function (carbon sequestration) with form (established meadow). It is clear there needs to be greater emphasis on defining restoration goals with these ecological functions/values in mind to improve local community buy in and ensure longer term success of a project. Native reference ecosystems have been postulated as a key driver of global restoration (McDonald et al. 2016) however in time, there may be the need to explore other reference ecosystems as climate change impacts are enforced. Finally, in Australia and globally there is increasing interest and investment in seagrass restoration and conservation, particularly with respect to growing national concerns around seagrass loss, erosion of 'blue carbon' stores, decline of fisheries and climate change impacts. This has led to a new community of research and practice being formed for seagrass restoration in Australia (Seagrass Restoration Network seagrassrestoration.net). As the practice of seagrass restoration develops, practitioners should adhere to National Standards for Ecological Restoration (McDonald et al. 2016) to align with global standards and consider adaptation required to make these applicable to seagrasses.

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# Chapter 21

# Global Warming and Ocean Acidification: Effects on Australian Seagrass Ecosystems

**Ylva S. Olsen, Catherine Collier, Yan X. Ow and Gary A. Kendrick**

**Abstract** As concentrations of atmospheric $CO_2$ increase, mean temperatures across the globe rise, the carbon system equilibrium in the ocean shifts, and pH is reduced in a process termed Ocean Acidification (OA). These changes can dramatically alter seagrass meadows as both temperature and pH fundamentally influence biochemistry and physiology of plants. Seagrass responses to climate change are species-specific and dependent on interactions with other factors such as light intensity, nutrient availability and competition. The majority of seagrasses appear limited by the availability of dissolved inorganic carbon at current ocean pH, suggesting that rates of photosynthesis and growth are likely to increase with OA. Short- and intermediate term laboratory experiments have shown an increase in photosynthetic rates to increased $p\mathrm{CO}_2$. Longer-term studies (>1 year) indicate enhanced shoot proliferation resulting in meadows with high shoot density. Studies utilizing natural gradients in $p\mathrm{CO}_2$ that exist near shallow volcanic $CO_2$ vents have shown that, overall, seagrasses appear to benefit from OA. Seagrasses photosynthesize across a range in temperatures, but rapidly decline above thermal optima.

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Respiration rates increase with warming at a faster rate than photosynthesis and reduces the overall photosynthesis-to-respiration ratio, and thus growth. While seagrasses can recover from moderate temperature stress, extreme temperatures result in mortality. Future changes in seagrass species distributions are predicted as sensitive species shift poleward. Foundation species, like seagrasses, have a large influence on their environment and their loss can significantly impact the functioning of the whole ecosystem. Despite a recent increase in climate-change research, we lack an understanding of how seagrass meadows are going to respond to the combined pressures of warming and OA. It is particularly difficult to predict longer-term responses and possible adaptation, and efforts should be focused in this area to determine how we can manage seagrasses to maximize resilience to climate change.

## 21.1 Introduction

### *21.1.1 Climate Change and Predictions*

Anthropogenic carbon emissions have led to a 40% increase in atmospheric levels of carbon dioxide ($CO_2$) since pre-industrial times (Raven et al. 2005) and the current rate of increase is higher than at any point during the last millennium (Doney and Schimel 2007). Predictions suggest that if no action is taken to curb $CO_2$ emissions, concentrations will increase from present-day atmospheric [$CO_2$] of ~400 ppm to ~1000 ppm by the year 2100 (Meehl and Stocker 2007; Fabry et al. 2008). The oceans absorb up to 50% of the atmospheric carbon emitted and 80% of the heat (Sabine et al. 2004; Levitus et al. 2001; Domingues et al. 2008) acting as a buffer to climate change, but also suffering the double effect of warming and ocean acidification. Along with other climate-related changes such as precipitation and runoff from land, wind patterns and storm frequency, these pressures will affect the productivity, distribution and phenology of marine organisms.

### *21.1.2 Carbon and Ocean Acidification*

The oceans sequester large amounts of $CO_2$ from the atmosphere (2 billion metric tons of carbon annually) and currently act as a net sink (Sabine et al. 2004; Sabine and Feely 2007). The consequence of increasing atmospheric $pCO_2$ and subsequent increase of $CO_2$ in the ocean ($CO_{2(aq)}$) is an increase in the concentration of hydrogen ions [$H^+$] in seawater or a lowering of the pH, termed ocean acidification (OA). Since the industrial revolution, oceanic pH has dropped by 0.1 units, which corresponds to a 30% increase in [$H^+$] (Orr et al. 2005; Fabry et al. 2008). Predictions for the end of the century based on the ‘business as usual’ scenario suggest that ocean surface waters will see a further reduction in pH by 0.3–0.4 units by 2100 (Orr et al. 2005). A change in pH creates a shift in the carbonate system equilibrium (Eq. 21.1; see also Chap. 11, Fig. 11.1), i.e.

the relative concentrations of dissolved inorganic carbon (DIC) species; $CO_{2(aq)}$, carbonic acid ($H_2CO_3$), bicarbonate ($HCO_3^-$) and carbonate ($CO_3^{2-}$):

$$CO_{2(aq)} + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons H^+ + CO_3^{2-} \tag{21.1}$$

Elevated $CO_{2(aq)}$ increases the total DIC (the sum of concentrations of the inorganic carbon species in Eq. 21.1) and [$H^+$] thus shifting the relative concentrations of the DIC species (Gattuso and Hansson 2011; Raven et al. 2005). At present, ocean pH is around 8.04 and $HCO_3^-$ is the dominant DIC species making up 89% (1650 µmol $kg^{-1}$ seawater) of the total pool whereas $CO_2$ only makes up 0.5% (8 µmol $kg^{-1}$ seawater) (Fabry et al. 2008; Koch et al. 2013). Assuming an increase in atmospheric $CO_2$ to a concentration of 1000 ppm by 2100, $HCO_3^-$ concentrations will increase more than $CO_2$ in absolute terms (mol $kg^{-1}$), but the proportion of $CO_2$ will see the greatest percent increase; >250%, compared to 24% for $HCO_3^-$ (Fabry et al. 2008; Koch et al. 2013). The large predicted relative increase in $CO_{2(aq)}$ is important for marine autotrophs including seagrasses that tend to have a higher affinity for $CO_2$ than $HCO_3^-$ (see Sect. 21.2.1.1; Madsen and Sand-Jensen 1991; Durako 1993). Although of less direct importance to seagrasses, it is also worth noting that the pool of $CO_3^{2-}$ is predicted to decline by more than 50%, which will have negative consequences for calcifying organisms (e.g. see Kroeker et al. 2010). The changes in the carbonate system are likely to have cascading consequences in marine ecosystems (Hofmann et al. 2010).

### 21.1.3 Warming

As concentrations of atmospheric $CO_2$ have risen, the mean surface temperature across the globe has increased by approximately 0.8 °C over the past century and 0.6 °C in the last three decades (Hansen et al. 2006). By 2100, temperatures are predicted to increase by a further 3–4 °C (Meehl and Stocker 2007). Rising sea surface temperature (SST) will pose challenges for marine macrophytes as biochemical processes and physiological functioning will be affected. A likely consequence of warming is the poleward shift of sensitive species, as has been recorded for temperate macroalgae along the Australian Pacific and Indian Ocean coastlines (Wernberg et al. 2011, in press).

Warming of the oceans is not spatially uniform and ‘hotspots’ have been identified where sea surface temperatures have been increasing at an accelerated rate. Higher than average warming is taking place in the coral triangle of the tropical Indo-Pacific presenting a risk to this biodiversity hotspot which includes 20% of the world’s 72 seagrass species (Waycott et al. 2004; Lough 2012). Temperatures off the SE and SW coasts of Australia have increased more than the global average over the past 50 years and the SE coastline is predicted to keep warming at an accelerated rate into the future (Hobday and Pecl 2014). Waters in SE Australia have a high level of fisheries production and host many endemic species. Additionally, there are no coastal areas to the south for vulnerable species to extend their range into. Major climate-related shifts have already been observed in this region, e.g. distribution patterns of Tasmanian fish (Last et al. 2011).

Superimposed on the pattern of overall warming of coastal waters are short-term thermal events called ‘heat waves’. The frequency and intensity of heat waves are predicted to increase as a consequence of climate change (Solomon et al. 2007). Western Australia experienced a marine heat wave along >2000 km of coastline reaching >200 km offshore in February and March 2011 with seawater temperature anomalies of +2 to 4 °C (Rose et al. 2012; Pearce and Feng 2013). The warming was associated with an unusually strong La Niña event, a record strength Leeuwin Current—the current that brings warm tropical waters southwards along the WA coast—and anomalously high air-sea heat flux into the ocean (Pearce and Feng 2013). Distribution, abundance and health of macroalgae, fish, corals (Wernberg et al. 2013), seagrasses and turtles (Fraser et al. 2014; Thomson et al. 2015) were heavily impacted by the marine heatwave.

## 21.2 Ocean Acidification

### *21.2.1 Carbon Metabolism and Photosynthesis*

#### 21.2.1.1 Inorganic Carbon Use

The responses of marine autotrophs to $CO_2$ depend on species-specific abilities to utilize different species of DIC. Utilisation of $HCO_3^-$ requires energy and is therefore less preferred to $CO_2$ as a carbon source (Burnell et al. 2014a; Hellblom and Axelsson 2003). However, the majority of DIC in seawater exists as $HCO_3^-$ at the current ocean pH of 8.04 (Fabry et al. 2008; Koch et al. 2013). A recent review of macroalgae and seagrasses by Koch et al. (2013) suggested that 95% of all marine macro-autotrophs are capable of using $HCO_3^-$ as substrate for photosynthesis. Out of the 72 known species of seagrass, 26 have been examined for bicarbonate use and the majority of these can use $HCO_3^-$ (Koch et al. 2013; Borum et al. 2016, Table 21.1). Bicarbonate use and other characteristics of 18 species of Australian seagrasses are summarized in Table 21.1. The majority of seagrasses tested, therefore, appear to exhibit relatively effective $HCO_3^-$ use. The ability to enhance C uptake through $HCO_3^-$ utilization is made possible because seagrasses employ a range of carbon concentrating mechanisms (CCMs), which are energetically costly. Energy is required to produce membrane-bound carbonic anhydrase (CA), which catalyses the dehydration of $HCO_3^-$ to $CO_2$ (Larkum et al. 1989). CA secretion into the cell wall appears to be fairly ubiquitous in seagrasses (Koch et al. 2013, Table 21.1), which may explain the large proportion of $HCO_3^-$ users among this group. Other CCMs include localised active $H^+$ extrusion to create $H^+$ gradients that facilitate the inward co-transport of $H^+$ and $HCO_3^-$, or a combined system in which extracellular

**Table 21.1** Photosynthetic pathways ($C_3$ or unknown (−)), the ability to use $HCO_3^-$, whether current seawater DIC concentrations are saturating for photosynthesis, presence of extracellular carbonic anhydrase (CA), and acidification of the diffuse boundary layer (DBL) for temperate and tropical Australian seagrasses

| Species | Temperate or tropical | Photosynthetic pathway | $HCO_3^-$ use | Saturated at current DIC[a] | Extracellular CA | Acidification of DBL | Reference |
|---|---|---|---|---|---|---|---|
| *Amphibolis antarctica* | Temp | – | No | No | No | No | 2 |
| *A. griffithii* | Temp | – | – | No | Yes | Yes | 2 |
| *Cymodocea rotundata* | Trop | – | Yes | No | Yes | – | 1 |
| *C. serrulata* | Trop | – | Yes | No | Yes | – | 1 |
| *Enhalus acoroides* | Trop | – | Yes | No | Yes | – | 1 |
| *Halodule uninervis* | Trop | $C_3$ | Yes | No | Yes | – | 1 |
| *Halophila ovalis* | Temp, Trop | – | Yes | No | Yes/No | No | 1, 2 |
| *H. spinulosa* | Trop | $C_3$ | Yes | – | Yes | – | 1 |
| *H. tricostata* | Trop | $C_3$ | – | – | – | – | 1 |
| *Posidonia australis* | Temp | – | Yes | No | Yes | Yes | 2 |
| *P. coriacea* | Temp | – | Yes | No | No | Yes | 2 |
| *P. sinuosa* | Temp | – | Yes | No | Yes | Yes | 2 |
| *Ruppia megacarpa* | Temp | – | Yes | No | Yes | Yes | 2 |
| *Syringodium isoetifolium* | Temp | $C_3$ | Yes | No | Yes/No | No | 1, 2 |
| *Thalassia hemprichii* | Trop | $C_3$ | Yes/No | No | Yes | – | 1 |
| *Thalassodendron ciliatum* | Trop | $C_3$ | Yes/No | No | Yes | – | 1 |
| *Zostera muelleri* | Temp | – | Yes | No | Yes | – | 1 |
| *Z. polychlamys* | Temp | – | Yes | Yes | Yes | Yes | 2 |

"Yes/No" indicates that different studies have found different results. Data from (1) Koch et al. (2013) (and references therein) and (2) Borum et al. (2016)

[a] Indicates that studies have found that current DIC concentrations saturate photosynthesis or not, but note that the photosynthetic response of seagrass to increased DIC depends on a multitude of other environmental and biological conditions (see Sect. 21.2.1.2)

CA-mediated $HCO_3^-$ conversion to $CO_2$ in acidic zones at $H^+$ extrusion sites, which concentrate $CO_2$ and facilitate diffusion into cells (Beer and Rehnberg 1997; Invers et al. 2001; Beer et al. 2002; Koch et al. 2013). Active transport relying on CA, conversion of $HCO_3^-$ to $CO_2$ and subsequent passive diffusion may be compromised at high pH, explaining why DIC limitation can occur at high pH even where $HCO_3^-$ is relatively high (Koch et al. 2013). There is also evidence suggesting that in macroalgae, high concentrations of $CO_{2(aq)}$ may lead to down-regulation of CCM activity and limit use of $HCO_3^-$ (Hepburn et al. 2011). Although the majority of seagrasses may be capable of utilizing $HCO_3^-$, there is a large degree of interspecific variation in dependency on the DIC substrates. Species differences are indicated by sensitivity to inhibitors of carbon-concentrating mechanisms (Schwarz et al. 2000; Invers et al. 2001; Uku et al. 2005; Campbell and Fourqurean 2013b; Borum et al. 2016; Ow et al. 2016a), responses to increasing $pCO_2$ (Borum et al. 2016) and the isotopic signatures of leaves, which may vary as a function of $HCO_3^-$ use because of its lower $\delta^{13}C$ compared to $CO_2$ (Raven et al. 1995; Hemminga and Mateo 1996; Raven et al. 2002).

#### 21.2.1.2 C-Limitation and Photosynthetic Responses to DIC Enrichment

The majority of seagrasses appear to be limited by DIC concentrations at current ocean pH despite being capable of utilizing the abundant $HCO_3^-$ (Koch et al. 2013; Borum et al. 2016; Chap. 11) due to the slow diffusion of $CO_2$ through the leaf boundary layer and possibly less efficient use of $HCO_3^-$ when compared to many macroalgal species (Beer 1989, 1994; Koch et al. 2013 although see Beer et al. 2002; Borum et al. 2016). Carbon-limitation at present $CO_2$ levels is probably attributed to the availability of $CO_{2(aq)}$ rather than $HCO_3^-$ (e.g. Borum et al. 2016). Addition of $CO_2$ enhances photosynthesis more than the addition of $HCO_3^-$ (Sand-Jensen and Gordon 1984; Durako 1993; Beer and Koch 1996; Invers et al. 2001; Burnell et al. 2014a) and the photosynthetic rates of four species of seagrass (*Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina* and *Phyllospadix torreyi*) were found to be $HCO_3^-$-saturated at concentrations well below those currently found in most seawater (Invers et al. 2001). Only three species—*Zostera polychlamis*, *Ruppia maritima* and *Zostera marina*—out of 25 tested were saturated at current ocean $p$CO$_2$ (*Z. marina* was found to be either or) (Koch et al. 2013; Borum et al. 2016). This suggests that rates of photosynthesis and growth are likely to increase under elevated $[CO_{2(aq)}]$.

Short- and intermediate term laboratory experiments have shown an increase in photosynthetic rates and optimization of photosynthetic performance e.g. lower light requirements, photosynthetic efficiency and pigment content in response to increased $p$CO$_2$ suggesting that low light impacts could be offset by increased C-availability (Zimmerman et al. 1997; Campbell and Fourqurean 2013b; Jiang et al. 2010; Russell et al. 2013; Ow et al. 2015). Seagrass species may, however, differ in the magnitude and manner in which they respond to $CO_2$ enrichment. For example, $p\mathrm{CO_2}$ enhancement of photosynthesis was higher in *Zostera marina* and *Phyllospadix torreyi* compared to *Posidonia oceanica* and *Cymodocea nodosa* (Invers et al. 2001). A study of nine temperate Australian seagrasses showed that net photosynthesis ($P_N$) of all but one species were C-limited at pre-industrial $CO_2$ levels (9 µM) compared to saturating $CO_2$ levels (274 µM or the equivalent of an atmospheric $CO_2$ of >8000 ppm) (Borum et al. 2016). Despite this, $CO_2$ enrichment to concentrations predicted for 2100 (24 µM) had a limited impact on $P_N$. Differences in the magnitude of the responses to $CO_2$-saturation among species were also detected, with larger species such as *Amphibolis antarctica*, *Posidonia sinuosa* and *Posidonia coriacea* responding relatively stronger compared to smaller species such as *Halophila ovalis* and *Ruppia megacarpa* (Borum et al. 2016). This implies that OA may change resource competition among co-occurring seagrasses growing in mixed beds, thereby potentially changing meadow structure and species dominance. A summary of data from studies of Australian seagrass responses to $CO_2$ enrichment is shown in Table 21.2.

**Table 21.2** Responses of Australian seagrass species to $CO_2$ enrichment. The highest $CO_2$ (or lowest pH) treatment, duration of experiment and responses measured are shown

| Species | Low pH/high $CO_2$ treatment | Duration | Resp | Reference | Comment |
|---|---|---|---|---|---|
| ***Net photosynthesis*** | | | | | |
| *Halophila ovalis* | 6.7, 274 µM $CO_2$ | 1–2 h | + | Borum et al. (2016) | |
| *Zostera polychlamys* | | 1–2 h | No | | |
| *Ruppia megacarpa* | | 1–2 h | + | | |
| *Amphibolis antarctica* | | 1–2 h | + | | |
| *Amphibolis griffithii* | | 1–2 h | + | | |
| *Posidonia australis* | | 1–2 h | + | | |
| *Posidonia sinuosa* | | 1–2 h | + | | |
| *Posidonia coriacea* | | 1–2 h | + | | |
| *Syringodium isoetifolium* | | 1–2 h | + | | |
| *Halophila ovalis* | 6.9 | 1–2 h | + | Russel et al. (2013) | |
| *Cymodocea serrulata* | | 1–2 h | + | | |
| *Cymodocea serrulata* | 7.45, 1948 µatm | 7 weeks | No | Collier et al. (in prep) | Data for 25 °C |
| *Halodule uninervis* | | 7 weeks | No | | |
| *Zostera muelleri* | | 7 weeks | + | | |
| *Cymodocea serrulata* | 7.71, 1013 µatm | 7 weeks | No | Collier et al. (in prep) | Data for 25 °C |
| *Halodule uninervis* | | 7 weeks | No | | |

(continued)

**Table 21.2** (continued)

| Species | Low pH/high $CO_2$ treatment | Duration | Resp | Reference | Comment |
|---|---|---|---|---|---|
| *Zostera muelleri* | | 7 weeks | No | | |
| *Cymodocea serrulata* | 7.76, 1204 µatm | 2 weeks | + | Ow et al. (2015) | |
| *Halodule uninervis* | | 2 weeks | + | | |
| *Thalassia hemprichii* | | 2 weeks | + | | |
| *Halodule uninervis* | 7.64, 1235 µatm | 3 weeks | + | Ow et al. (2016b) | |
| *Thalassia hemprichii* | | 3 weeks | No | | |
| *Halophila ovalis* | 7.8, 800 µM $CO_2$ | 1–2 h | No | Borum et al. (2016) | |
| *Zostera polychlamys* | | 1–2 h | No | | |
| *Ruppia megacarpa* | | 1–2 h | No | | |
| *Amphibolis antarctica* | | 1–2 h | No | | |
| *Amphibolis griffithii* | | 1–2 h | No | | |
| *Posidonia australis* | | 1–2 h | No | | |
| *Posidonia sinuosa* | | 1–2 h | No | | |
| *Posidonia coriacea* | | 1–2 h | No | | |
| *Syringodium isoetifolium* | | 1–2 h | No | | |
| *Amphibolis antarctica* | 7.82 | 12 weeks | + | Burnell et al. (2014a, b) | |
| *Halodule uninervis* | 7.82, 1077 µatm | 2 weeks | No | Ow et al. (2016a) | |
| *Cymodocea serrulata* | | 2 weeks | No | | |
| *Halodule uninervis* | 7.83, 731 µatm | 3 weeks | + | Ow et al. (2016b) | |
| *Thalassia hemprichii* | | 3 weeks | No | | |
| ***Leaf growth*** | | | | | |
| *Thalassia hemprichii* | 6.20 | 2 weeks | + | Jiang et al. (2010) | |
| *Cymodocea serrulata* | 7.29, 5098 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.32, 2754 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.45, 1948 µatm | 7 weeks | + | Collier et al. (in prep) | Temperature interactions, Data for 25 °C |
| *Halodule uninervis* | | 7 weeks | No | | |
| *Zostera muelleri* | | 7 weeks | No | | |

(continued)

**Table 21.2** (continued)

| Species | Low pH/high $CO_2$ treatment | Duration | Resp | Reference | Comment |
|---|---|---|---|---|---|
| *Thalassia hemprichii* | 7.50 | 2 weeks | + | Jiang et al. (2010) | |
| *Cymodocea serrulata* | 7.57, 1550 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| *Halodule uninervis* | pH = 7.64, 1235 µatm | 3 weeks | + | Ow et al. (2016b) | Nutrient interactions |
| *Thalassia hemprichii* | | 3 weeks | +/- | | |
| *Cymodocea serrulata* | 7.65, 1252 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.74, 966 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.75, 918 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Thalassia hemprichii* | 7.75 | 2 weeks | + | Jiang et al. (2010) | |
| *Cymodocea serrulata* | 7.76, 1204 µatm | 2 weeks | + | Ow et al. (2015) | |
| *Halodule uninervis* | | 2 weeks | + | | |
| *Amphibolis antarctica* | 7.82 | 12 weeks | + | Burnell et al. (2014a, b) | |
| *Halodule uninervis* | 7.82, 1077 µatm | 2 weeks | +/- | Ow et al. (2016a) | Light interactions |
| *Cymodocea serrulata* | | 2 weeks | + | | |
| *Halodule uninervis* | 7.83, 731 µatm | 3 weeks | +/- | Ow et al. (2016b) | Nutrient interactions |
| *Thalassia hemprichii* | | 3 weeks | No | | |
| *Cymodocea serrulata* | 7.92, 548 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.93, 543 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| ***Biomass*** | | | | | |
| *Cymodocea serrulata* | 7.29, 5098 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.45, 1948 µatm | 7 weeks | No | Collier et al. (in prep) | Temperature interactions, Data for 25 °C |
| *Halodule uninervis* | | 7 weeks | No | | |
| *Zostera muelleri* | | 7 weeks | No | | |
| *Cymodocea serrulata* | 7.57,1550 µatm | $CO_2$ seeps | No | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.65, 1252 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |

(continued)

**Table 21.2** (continued)

| Species | Low pH/high $CO_2$ treatment | Duration | Resp | Reference | Comment |
|---|---|---|---|---|---|
| *Cymodocea serrulata* | 7.75, 918 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.92, 548 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |
| *Cymodocea serrulata* | 7.93, 543 µatm | $CO_2$ seeps | + | Takahashi et al. (2015) | |

## *21.2.2 Productivity and Biomass*

Enhanced photosynthetic rates associated with $CO_2$ enrichment could theoretically have flow-on effects for plant performance and growth. In almost all cases, experimental $CO_2$ enrichment has been associated with some biochemical changes such as increasing carbohydrate content of below-ground storage (rhizomes), changes in N and P content, and changes in $\delta^{13}C$ (Campbell and Fourqurean 2013a; Jiang et al. 2010; Ow et al. 2016b). Growth and biomass responses, however, are more variable. Leaf growth is usually responsive in short-term experiments, but not consistently among species. For example, *Cymodocea serrulata*, *Halodule uninervis* and *Thalassia hemprichii* showed an increase in net productivity, maximum photosynthetic rates ($P_{max}$) and efficiency ($\alpha$) after 2 weeks of exposure to increased $p$CO$_2$, but leaf growth rates only increased for *H. uninervis* and *T. hemprichii* (Ow et al. 2015). A study by Jiang et al. (2010) showed a >2.6% increase in leaf growth of *Thalassia hemprichii* after 3 weeks exposure to pH 7.76, but Campbell and Fourqurean (2013a) found no effect of $CO_2$ enrichment on growth of *T. testudinum*.

Longer-term studies (>6 months) suggest that enhancement of leaf growth rate is not typically maintained (Campbell and Fourqurean 2013a; Palacios and Zimmerman 2007), though with some variability (Takahashi et al. 2015). In fact, specific growth rates may even decline at elevated $p$CO$_2$, due to larger shoots taking longer to turnover (Takahashi et al. 2015). Differences in the responses to $CO_2$ enrichment among species could be partially explained by differences in DIC uptake mechanisms (see Sect. 21.2.1.1), carbon allocation e.g. investment in production of new shoots or growth of existing tissue and above- versus belowground biomass, and leaf turnover (Ow et al. 2015; Takahashi et al. 2015).

Longer-term studies (>1 year) indicate that biomass production is more commonly enhanced through rhizome extension and branching (shoot proliferation) (Palacios and Zimmerman 2007), which means that seagrass meadows exposed to long-term enrichment tend towards a high shoot density (Hall-Spencer et al. 2008; Fabricius et al. 2011; Takahashi et al. 2015). These studies highlight that responses of seagrasses to increased $p$CO$_2$ are not easy to predict, both in the short and the long term. For most seagrass species the responses to increased $p$CO$_2$ are still unexplored. One of the reasons for this is the difficulty in assessing long-term effects due to the logistics, time and cost associated with long-term $CO_2$ enrichment experiments. Attempts to better characterise long-term exposure of whole communities, including seagrass meadows, to elevated $pCO_2$ have been made by utilizing natural gradients in $pCO_2$ that exist near shallow volcanic $CO_2$ vents (see BOX). These studies have shown varying effects of long-term exposure, but overall, seagrasses appear to benefit from acidification of seawater (Hall-Spencer et al. 2008; Fabricius et al. 2011; Russell et al. 2013, but see Apostolaki et al. 2014).

### *21.2.3 Volcanic Vents as a Case Study*

At volcanic $CO_2$ vents, streams of gas bubbles emerge from the seafloor reducing the pH of the water column. Gradients of pH are produced across distances of tens of meters until the signal is completely suppressed by mixing with seawater of natural pH. These seeps and vents occurring in shallow coastal habitat provide a natural laboratory to investigate effects of long-term exposure and adaptation to high $CO_2$ in situ and offer significant advantages over laboratory experiments, which are often based on single species and single life-stages. Temperate shallow-water volcanic $CO_2$ vents in the Mediterranean and a tropical vent system in the Indo-Pacific have been studied, including Ischia and Vulcano Islands in Italy, where pH reaches values as low as 6.6–6.8 (Hall-Spencer et al. 2008; Apostolaki et al. 2014), and volcanic seeps in Papua New Guinea with pH values $<7.7$ (as low as 7.21) (Fabricius et al. 2011). Elevated $CO_{2(aq)}$ near the vents appears to have caused declines and changes in community structure in many calcifying and non-calcifying organisms, including corals and crustose coralline algal epiphytes on seagrass leaves, whereas some fleshy macroalgae and seagrasses appear to be favored by reduced seawater pH, showing increased shoot density and an increase in belowground biomass (Hall-Spencer et al. 2008; Fabricius et al. 2011).

Within seagrass meadows at the Papua New Guinea seeps, which are within the same biogeographic region as northern Australia (i.e. species composition overlaps with that of tropical Australia), pH can reach below 7.3, and $\delta^{13}C$ signatures indicate a strong effect of seep $CO_2$ on photosynthetic C-uptake (Takahashi et al. 2015). Higher rates of productivity were measured at seep compared to ambient pH sites (Russell et al. 2013). Biomass was increased by more than 5-fold at seep sites compared to control sites, including the belowground biomass, thus demonstrating the potential for enhanced C-storage through seagrass carbon uptake (Fabricius et al. 2011; Russell et al. 2013; Takahashi et al. 2015). The diversity of species was also affected: the canopy-forming species *Cymodocea serrulata*, *C. rotundata* and *Halodule uninervis* dominated at seep sites, and *Halophila ovalis* only occurred at control sites and was completely absent near the seeps. These differences may relate to interspecific variation in inorganic carbon utilization, or may indicate competitive exclusion at extremely high biomass (Takahashi et al. 2015).

*Posidonia oceanica* meadows growing around the Ischia vents in the Mediterranean are exposed to pH as low as 7.4 (Hall-Spencer et al. 2008). Shoots were at least 10 years old, so had integrated the effects of acidification over this time. Shoot density was higher at the acidified end of the $CO_2$ gradient (>1000 shoots $m^{-2}$ compared to 500–600 shoots $m^{-2}$ at normal pH) and leaves had only 2% cover of calcified epiphytes compared to 75% at the control site (Hall-Spencer et al. 2008). Additionally, shoots transplanted from the control site showed complete dissolution of *Corallinaceae* in two weeks. High $p\mathrm{CO}_2$ enhanced productivity of *P. oceanica*, but no evidence of photosynthetic performance was found.

*Cymodocea nodosa* growing in acidified water at Vulcano also had reduced $\delta^{13}C$ signatures indicative of uptake of vent $CO_2$ (Apostolaki et al. 2014). The high $p\mathrm{CO}_2$ stimulated photosynthetic activity (e.g. increased maximum electron transport rate and compensation irradiance) and leaves had higher chlorophyll content. Community metabolism including net primary production was also enhanced in the acidified meadow, but conversely to what was found at Papua New Guinea seeps and Ischia vents, this was not translated into higher seagrass biomass. Shoot density and biomass were lower and the ratio of above- to belowground biomass was increased tenfold. This was probably due to nutrient limitation, grazing or poor environmental conditions (Apostolaki et al. 2014).

Increased seagrass growth may not always translate into higher biomass near $CO_2$ vents due to intense 'top down' control. Large herbivorous fish (*Sarpa salpa*) were observed grazing selectively on seagrass growing near the vents at Ischia and Vulcano. In fact, at the most acidified locations in Vulcano, canopy height was reduced to around 50% (Apostolaki et al. 2014, Fig. 21.1b). This could be linked to the loss of phenolic substances in seagrass growing in high $p\mathrm{CO}_2$ environments (Arnold et al. 2012) or the lower abundance of calcareous epiphytes on leaves (Hall-Spencer et al. 2008), which may render them more palatable to grazers

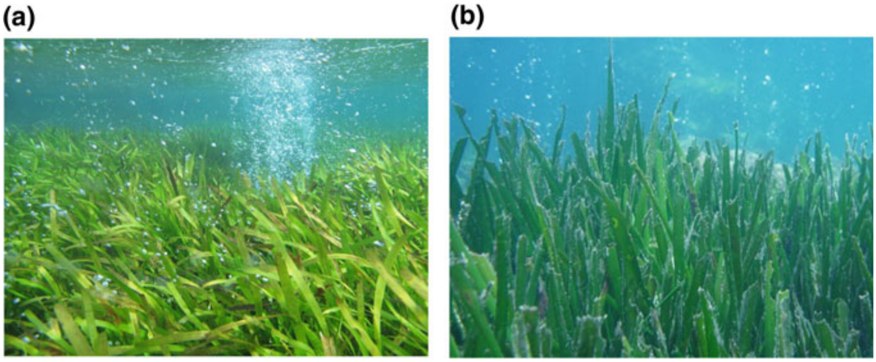


**Fig. 21.1** **a** $CO_2$ emerging from the seafloor at the Illi seeps, Papua New Guinea. *Photo* C. Collier. **b** Evidence of heavy grazing on *Posidonia oceanica* at the Ischia $CO_2$ vents, Italy. *Photo* Y. S. Olsen

(Apostolaki et al. 2014). The benefits from $CO_2$ enrichment to seagrasses at the vents may therefore be partly counteracted by intense top-down control.

Naturally $CO_2$-enriched systems offer a unique opportunity to look at whole-system responses to OA and, as demonstrated by the examples above, have given us evidence of broad trends in responses of calcifiers and producers including seagrasses. They have also revealed complex species-specific and site-specific responses, e.g. shifts in species composition and above-to belowground biomass and changes in interaction strength between seagrasses and herbivores that would have been difficult to predict from small-scale aquarium or mesocosm studies.

## *21.2.4 Effects of Seagrass on pH*

### 21.2.4.1 Coastal Variability in pH

Coastal oceans are characterized by large natural variability in carbonate chemistry and pH, unlike pH in the open ocean, which tends to be more stable (Hofmann et al. 2011; Mercado and Gordillo 2011; Duarte et al. 2013). Anthropogenic inputs of $CO_2$ play a smaller role in coastal waters relative to other sources of variability, such as watershed and metabolic effects (Duarte et al. 2013; Uthicke et al. 2014). Observations of pH in a variety of coastal habitats indicate characteristic site-specific diurnal, semi-diurnal and stochastic patterns of varying amplitudes (Hofmann et al. 2011; Duarte et al. 2013). In highly productive ecosystems, this variability is largely driven by metabolic activity as pH values increase during the day when $CO_2$ uptake through photosynthesis is high and decrease at night due to $CO_2$ release from respiration (Fig. 21.2). The magnitude of this effect depends on the productivity of autotrophs as well as on the residence time of water in the vegetated area (Hendriks et al. 2014). Vegetated habitats alter water flow, attenuate waves and turbulence and increase the residence time of water (Granata et al. 2001; Hendriks et al. 2008; Frieder et al. 2012), thereby amplifying the metabolic signal. Seagrass meadows, mangroves, salt marshes, coral reefs and macroalgal beds can support diel changes in pH as high as 1.0 unit (summarized in Duarte et al. 2013) and pH-variations outside of these habitats are significantly lower (Delille et al. 1997).

### 21.2.4.2 Metabolic Activity and pH in Seagrass Meadows

Seagrass meadows are highly productive and have the ability to modify pH in the surrounding water by as much as 0.5–0.7 pH units diurnally through photosynthetic activity and community metabolism (Frankignoulle and Distèche 1984; Frankignoulle and Bouquegneau 1990; Invers et al. 1997). The pH variation follows patterns of photosynthetically active radiation (PAR) and is strongly correlated to concentrations of dissolved oxygen. In the Mediterranean, diurnal ranges of 0.3

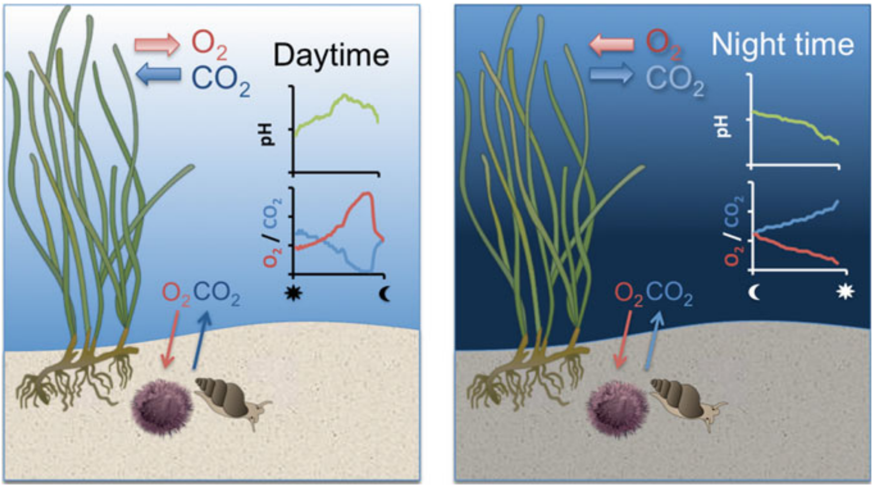


**Fig. 21.2** Conceptual diagram of how producers modify pH by photosynthesis and metabolic activity. Arrows indicate net consumption and production of $O_2$ and $CO_2$. Inset graphs show typical changes in pH (top) and $O_2$ and $CO_2$ (bottom) between sunrise and sunset (daytime, left) and between sunset and sunrise (nighttime, right). *Image credit* seagrass and sea urchin—T. Saxby, gastropod—D. Tracey, IAN Image Library (http://ian.umces.edu/imagelibrary)

pH units (8.15–8.45) were measured in the water column above shallow *Posidonia oceanica* meadows, and 0.48 pH units (8.11–8.59) in *Cymodocea nodosa* meadows (Invers et al. 1997). In shallow *Posidonia oceanica* meadows (5–12 m) diel changes of pH, DIC, net aragonite saturation state ($\Omega_{Ar}$) and $O_2$ were observed with the magnitude of pH variation in summer, near the peak of productivity, being much higher (0.24 pH units) compared to in autumn (0.06 pH units) (Hendriks et al. 2014). The magnitudes of these diurnal cycles were related to structural parameters of the meadow, in particular, the leaf surface area available for photosynthesis (LAI), which was positively correlated to the mean and maximum pH measured and the maximum $\Omega_{Ar}$. The influence of the seagrass community metabolism reached beyond the meadow to bare areas where clear diurnal signals of around 0.05 pH units were observed (Hendriks et al. 2014). Similar ranges of around 0.2–0.3 pH units have been observed in meadows of *Thalassia testudinum* in Bermuda (Schmalz and Swanson 1969) and in *Posidonia sinuosa* in Western Australia (Olsen unpublished data, Fig. 21.3). The influence on the water column is diluted with increasing distance from the meadow (Invers et al. 1997) although a clear metabolic signal could be detected in pH measured at the water surface above an 8 m deep *P. oceanica* meadow (Frankignoulle and Distèche 1984) suggesting that the influence of the meadow stretches far beyond the canopy itself.

Modification of pH by macrophytes is further enhanced in enclosed or semi-enclosed bodies of water with low water exchange rates. *Thalassia hemprichii* and *Enhalus acoroides* were found to be living on the edge of their tolerances in rockpools characterized by extreme tides and diel temperature amplitudes where

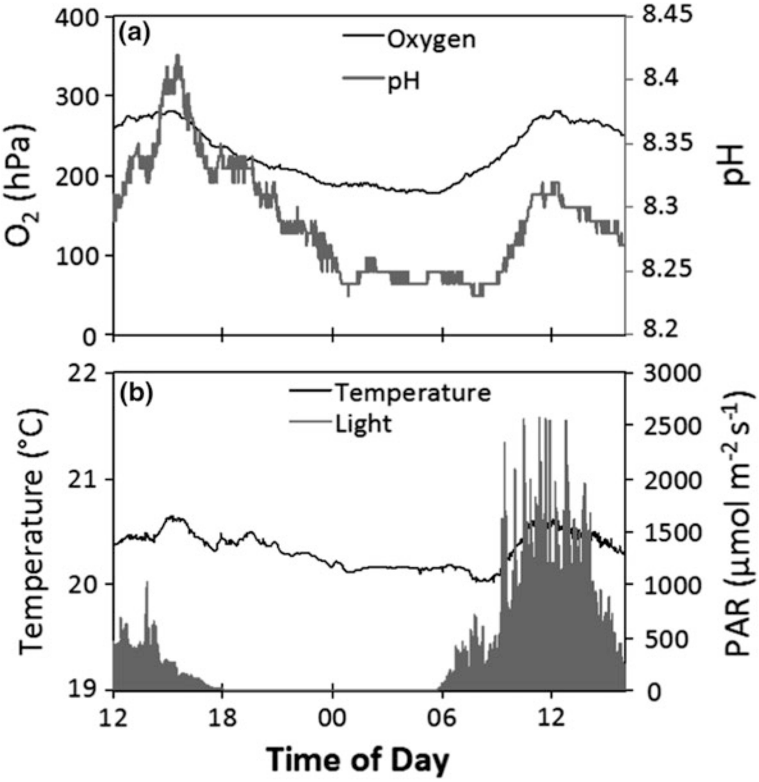


**Fig. 21.3** Diurnal pattern of **a** water column $pO_2$ and pH and **b** incident light and temperature at canopy height in a *Posidonia sinuosa* meadow off Garden Island, Western Australia. Metabolic processes in the meadow drive $pO_2$ and pH as $CO_2$ is taken up and $O_2$ released and closely mirror diurnal levels of PAR (data from Y. S. Olsen, unpublished)

temperature reached 38 °C and pH could be as high as 8.8 during daytime low tide when photosynthesis was intense (Pedersen et al. 2016). Diurnal fluctuations >1 pH unit were observed in a semi-enclosed seagrass system with low water exchange rates in Chwaka bay, Tanzania (Semesi et al. 2009). The highest pH values were recorded during low tide, and coincided with low total alkalinity and low dissolved inorganic carbon concentrations. In the same system, photosynthesis by the seagrasses *Halophila ovalis*, *Cymodocea rotundata* and *T. hemprichii* raised the pH in tide pools to 8.5, 8.7 and 9.0 respectively (Beer et al. 2006). The altered carbonate chemistry in these extreme environments can negatively affect the photosynthetic performance of other producers, e.g. metabolism of *Ulva intestinalis* in rockpools was found to exclude other macroalgae (Björk et al. 2004) and *H. ovalis* was unable to grow in intertidal pools together with other seagrasses that raised the pH beyond its compensation point (Beer et al. 2006).

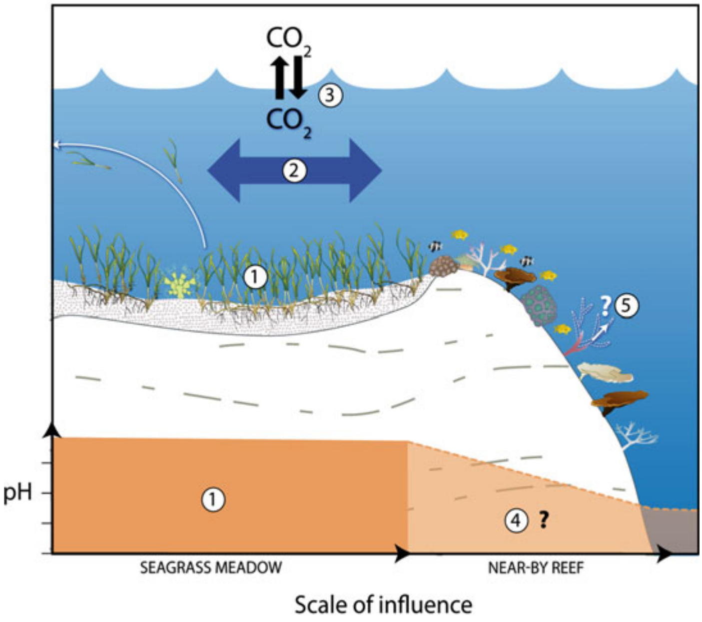
Seagrasses also play an important role in controlling interstitial porewater pH and rates of carbonate dissolution in sediments of shallow tropical systems. Transport of oxygen from the leaves to the rhizosphere during photosynthesis increases dissolution of carbonate sediment leading to increased alkalinity, dissolved inorganic carbon and $Ca^{2+}$ but decreased pH in porewaters (Morse et al. 1987; Burdige and Zimmerman 2002). The rates of dissolution may be a significant loss to the overall carbonate budget of shallow-water carbonate platforms and many exert a negative feedback on rising atmospheric $CO_2$ (Burdige et al. 2008).

#### 21.2.4.3 Can Autotrophs Provide Buffers Against OA?

Marine organisms in metabolic-intense habitats are experiencing pH that is significantly different from that of the surrounding bulk water. Regulation of pH due to metabolic activity may thus provide a chemical ‘refuge’ for organisms by raising minimum or maximum pH, limiting the time spent below some critical pH threshold or increasing net aragonite saturation state ($\Omega_{Ar}$) (Kleypas et al. 2011; Manzello et al. 2012; Hendriks et al. 2014) (Fig. 21.4). A model based on records of seagrass metabolism in the Indo-Pacific suggested that increases of up to 0.38 pH units, and $\Omega_{Ar}$ of 2.9 in seagrass meadows could potentially enhance calcification of scleratinian corals downstream of seagrasses by 18% (Unsworth et al. 2012). There is also some evidence that macroalgae may benefit from seagrass metabolic processes. High pH values caused naturally by seagrass photosynthesis enhanced calcification rates of the calcareous red macroalgae (*Hydrolithon* sp. and *Mesophyllum* sp.) and the green macroalga (*Halimeda renschii*) growing within a tropical seagrass bed where daytime pH could reach values >8.9 due to the semi-enclosed nature of the site (Semesi et al. 2009).

### *21.2.5 OA and Resilience*

Seagrasses appear to have the ability to acclimate to increasing $CO_2$ and changes in pH, and conditions for seagrasses may improve in a high $pCO_2$ world. Nevertheless, maintaining genetically diverse populations under climate change is important as other stressors may occur alongside OA (Sects. 4 and 5). We do not know how OA will affect genetic diversity in seagrass meadows. Eelgrass *Zostera marina* exposed to elevated $CO_2$ increased vegetative proliferation of shoots, rhizome elongation and branching (Palacios and Zimmerman 2007), but also enhanced reproductive output (as % flowering shoots), presumably because increased DIC concentrations allowed the plants to invest in energetically costly reproductive structures. Clearly the hypothesis that genetic diversity would be reduced by OA found little support from this single study. OA also appears to enhance seedling survival and performance (Burnell et al. 2014b), which would also serve to maintain and enhance genetic diversity.



1. High net production in seagrass meadows alters seawater DIC equilibrium and may benefit nearby organisms by raising pH and calcite and aragonite saturation states (Beer et al. 2006, Unsworth et al. 2012, Hendriks et al. 2014).
2. Seagrasses alter flow and increase the residence time of water (Granata et al. 2001, Hendriks et al. 2008) thereby strengthening the metabolic signal of the water. The metabolic influence can reach beyond the meadow itself (Frankignouille and Distèche 1984, Invers et al. 1997).
3. Air/water exchange of $CO_2$ affects seawater carbonate equilibrium (e.g. Fabry et al. 2008) and future increases of atmospheric $pCO_2$ may increase seagrass productivity (Hall-Spencer et al. 2008, Fabricius et al. 2011, Russell et al. 2013).
4. Effects of seagrass metabolism on the carbonate chemistry at broader spatial scales remain uncertain.
5. Effects on calcification of corals and other calcifying organisms are uncertain, but can be positive in enclosed or semi-enclosed environments (Semesi et al. 2009).

**Fig. 21.4** Schematic of the influence of seagrass metabolism on the carbonate chemistry of adjacent habitats

Seagrasses growing along a natural pH gradient near volcanic $CO_2$ seeps in Papua New Guinea show reduced diversity at high $pCO_2$ (Fabricius et al. 2011, Takahashi et al. in press). Canopy-forming *Cymodocea serrulata*, *C. rotundata* and *H. uninervis* dominate at reduced pH, whereas *Halophila ovalis* only grows at control sites with normal pH. Similarly, *Cymodocea nodosa* and *Zostera noltii* were both found growing at control sites outside the influence of the $CO_2$ vent in Vulcano, Italy, whereas *Z. noltii* was absent from areas enriched by $pCO_2$ (Apostolaki et al. 2014). It is therefore possible that OA will affect species diversity within meadows as some species are more successful at competing for the increased resources. Changes in species diversity could affect the ecosystem services provided by seagrass meadows (Unsworth et al. 2015; Kilminster et al. 2015), however the very limited data available on population-level effects of OA prevents us from making strong predictions.

## 21.3 Warming

### *21.3.1 Metabolism*

#### 21.3.1.1 Photosynthesis

Seagrasses have a broad thermal window for photosynthesis, being able to photosynthesise from 0 °C through to 45 °C depending on the species and on acclimation to local conditions (Dennison 1987; Lee et al. 2007; Pedersen et al. 2016). Seagrass photosynthesis rises slowly with temperature then increases more quickly to an optimum (see Sect. 21.3.3). Acclimation to high temperature occurs by improving the heat stability of the photosynthetic apparatus (Bita and Gerats 2013; Yamori et al. 2014). The rapid rise is approximately exponential and is described by $Q_{10}$—the rate of change for every 10 °C—and this is a useful parameter to quantify the temperature-dependent relationship of photosynthesis in ecological models and to describe acclimation to ocean warming. At extremely high temperatures, heat-shock proteins (HSPs) are also produced to stabilize membranes and proteins (Yamori et al. 2014). Zeaxanthin-facilitated thermal energy dissipation (photochemical quenching) responds rapidly (after only 5 h of exposure) to elevated temperature as a means to protect the photosystems from accumulations of reactive oxygen species (ROS) (Ralph 1998; Demmig-Adams 2003). Despite these acclimatory processes, rapid declines in photosynthetic rate occur at temperatures above thermal optima (Yamori et al. 2014; Adams et al. 2017; Pedersen et al. 2016) triggering temperature stress. Rubisco—the first enzyme involved in carbon fixation —is deactivated and Rubisco activase repair activity declines (Salvucci and Crafts-Brandner 2004). Furthermore, oxygenation of ribulose biphosphate (RuBP) by Rubisco (photorespiration) increases with temperature and reduces the efficiency of carbon fixation (Koch et al. 2013).

Photosystem II (PSII) is particularly sensitive to warming (Ralph 1998) and effective quantum yield has been applied to assess temperature stress in seagrasses. Campbell et al. (2006) measured reduced photosynthetic yield (Fv/Fm) in response to short-term heat stress (3 days of 4 h exposure of >40 °C) in *Halophila ovalis*, *Zostera capricorni* and *Syringodium isoetifolium*. In contrast, no detrimental response was found in *Cymodocea rotundata*, *C. serrulata* and *H. uninervis* suggesting these species have a wider tolerance to warming. For all species examined, warming induced a decline in maximum fluorescence, Fm′, which represents photoinhibition due to closure of PSII reaction centres and chloroplast dysfunction

(Campbell et al. 2006). Seagrasses photoacclimate to optimise photosynthetic rates over increasing temperature; however this is dependent on a number of other conditions, including incoming light. Photosynthetic efficiency at light-limiting irradiance ($\alpha$) is not usually affected by increasing temperature over the "optimal range" for photosynthesis (Bulthuis 1983; Staehr and Borum 2011; Collier et al. 2017) with some exceptions (Masini et al. 1995). However, up-regulation of maximum photosynthetic rates ($P_{max}$), enable seagrasses to reach higher rates of photosynthesis at increasing temperature (Bulthuis 1983; Staehr and Borum 2011; Collier et al. in prep). Thus, a higher light level is required to saturate photosynthesis i.e. $I_k$, the half-saturation constant increases with temperature (Masini et al. 1995). Conversely, high light allows seagrass to withstand higher temperatures (Bulthuis 1987). This has been confirmed for tropical species that tend to live close to their physiological optimum, but are able to maintain high photosynthetic rates at elevated temperatures as long as there is sufficient light (e.g. Collier et al. 2011).

Recovery from temperature stress depends upon the magnitude of the thermal shock including both temperature anomaly and duration of exposure (Bulthuis 1987). For example, *H. ovalis* from Sydney Harbour was able to fully recover after 5 days from moderate heat stress (at 27.5 and 30 °C, compared to ambient at 25 °C) that reduced photosynthetic efficiency by 30%, most likely by synthesis of new proteins (Ralph 1998). However, irreversible damage to PSII prevented recovery at 32.5 and 35 °C after 5 days. By contrast, a northern population (Green Island, Cairns) of *H. ovalis* recovered from photosystem stress at 40 °C within 2 days (Campbell et al. 2006), even though exposure to this temperature is high enough to induce some shoot mortality (Collier and Waycott 2014). Temperatures of 43–45 °C (after 4 h exposure) result in irreversible damage and mortality in all tropical species tested to date (Campbell et al. 2006; Collier and Waycott 2014; Pedersen et al. 2016).

#### 21.3.1.2 Respiration

Respiration is central to growth, as it provides the energy for cell maintenance and biosynthesis. Therefore, understanding respiratory pathways and controls of respiration are vital to the advancement of seagrass growth models that predict responses to future warming. While respiratory metabolic pathways have not been extensively described in seagrasses, controls on respiratory rates, in particular temperature controls on respiration have been tested for some species. In seagrasses, respiration rates increase with temperature with the rate of increase over a narrow range of typical in situ temperatures (around 10–40 °C depending on species and habitat) being linear (Collier et al. in prep) or exponential (Perez and Romero 1992; Pedersen et al. 2016; Collier et al. in prep) (Fig. 21.5). This rise can be driven by the production of stress proteins (such as heat-shock proteins) and the production of mitochondria (Koutalianou et al. 2015). Respiration rates and the rate of increase with temperature ($Q_{10}$) are higher in seagrass leaves than in the below-ground non-photosynthetic structures (Fourqurean and Zieman 1991; Collier et al. in prep) which is typical for higher plants (Atkin et al. 2005). This increases the demand for oxygen, particularly to below-ground structures in low oxygen sediments (Pedersen et al. 2016), with lowest sediment oxygen occurring at sunrise, after respiration has depleted throughout the night (Borum et al. 2005). Respiration rates decline at extreme temperatures (e.g. Collier et al. in prep) (Fig. 21.5), however this is rarely observed in seagrasses owing to the paucity of data on the temperature-dependency of respiration, and the relatively high temperature tolerance of seagrasses meaning that these extreme temperatures are not usually tested. Physiological acclimation can slow the rate of respiratory rise ($Q_{10}$) and this can be driven by passive response (e.g. reduced substrate availability), but it may also be critical in helping plants survive under changing temperatures and this needs to be more fully explored in order to model future change (Atkin et al. 2005).

#### 21.3.1.3 Net Productivity

Net primary production is the overall energetic surplus resulting from photosynthesis, respiration and photorespiration. Photoacclimation and increasing photosynthesis at higher temperatures is somewhat offset by the increased respiratory carbon loss from antioxidative activity (Massa et al. 2011) and other repair processes at elevated temperatures. Therefore net productivity increases more slowly with temperature (has a lower $Q_{10}$), and a lower thermal optima than photosynthesis (Collier et al. in prep) (Fig. 21.5). The effects of warming on net productivity are exacerbated by environmental conditions that reduce photosynthetic activity, such

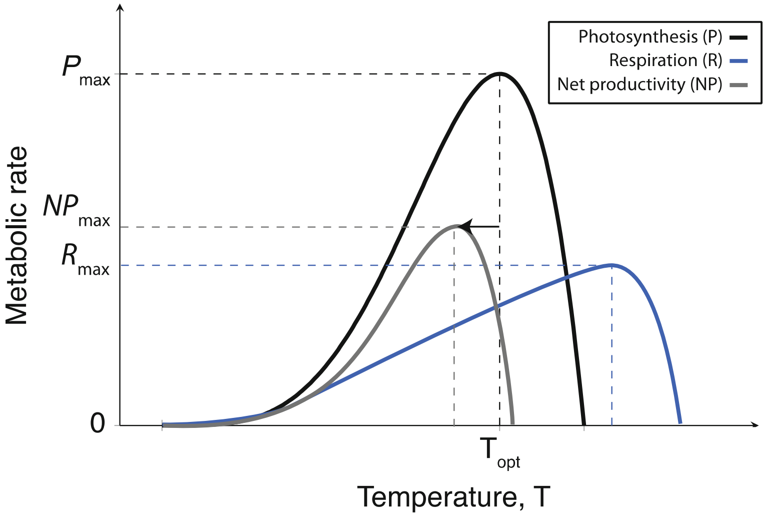


**Fig. 21.5** Theoretical metabolism-temperature response curve for photosynthesis, respiration and net productivity. Adapted from Staehr and Borum (2011), Adams et al. (2017) and Collier et al. (2017)

as low light (Collier et al. 2011). Chronic increases in temperature could reduce net primary production and drive declines in seagrass growth and density.

### 21.3.2 Growth, Shoot Morphology, Above-Belowground Allocation

Photosynthesis and respiration are temperature-dependent metabolic processes and the balance between these processes (net productivity) determines the rate of growth and seagrass meadow development (e.g. Millar et al. 2011). However, a range of different factors regulates growth, morphology and biomass allocation in seagrasses and it can be hard to identify the role of temperature in situ. Growth rates are highly variable among Australian species and leaf extension times and leaf turnover times reflect their life-history strategies (Kilminster et al. 2015), such that persistent species grow slowly (Marbà and Walker 1999) and colonizing species grow very rapidly (Walker et al. 1999; McMahon 2005). Optimum temperatures for growth are typically lower than those for photosynthesis (Lee et al. 2007) as respiration increases with warming at a faster rate so that the overall photosynthesis-to-respiration ratio is reduced. As seen for photosynthesis, tropical species have higher average optimum temperatures for growth (23–32 °C) compared to temperate species (11.5–26 °C) (Lee et al. 2007). Growth and shoot production can respond very strongly to changing temperature (Ehlers et al. 2008). For example, *C. serrulata*, *H. uninervis* and *Z. muelleri* increased leaf extension rates by 2–3 times after exposure to increasing temperature from 20 to 25 °C or 30 °C (similar to ambient seasonal range) for seven weeks (Collier et al. 2011; Collier et al. in prep) and *H. ovalis* linearly increased growth from 0 mgDW $\text{apex}^{-1}\ \text{d}^{-1}$ at 10 °C to 2 mgDW $\text{apex}^{-1}\ \text{d}^{-1}$ at 25 °C (also similar to ambient seasonal range).

Seasonal growth measures in situ provide further indication of the effect of temperature on growth. Growth was more than four times faster in *Posidonia australia* in summer (February) compared to winter (June) (Cambridge and Hocking 1997) but the seasonal variation can be even higher in colonizing and opportunistic species (Hillman et al. 1995). Seasonal growth and thermal optima are strongly affected by incoming light (Bulthuis 1987; Collier et al. in prep; Collier et al. 2007) and growth models that account for only temperature and light provide a reasonable estimation of in situ growth rates (Pérez and Romero 1992; Hillman et al. 1995); however, other local factors also influence seasonal growth (Alcoverro et al. 1995).

Seagrass growth rates decline from chronic (Collier et al. 2017) or acute temperature stress (Collier and Waycott 2014). Morphological adjustments and biomass loss (shoot mortality, leaf senescence) also occur, which may also help to restore metabolic balances in the plant. For example, leaf width and biomass declined at 30 °C compared to 24 and 27 °C for *Z. muelleri* (York et al. 2013).

Early life history stages are also vulnerable, as the regulation of respiratory pathways during plant development is limited (van Dongen et al. 2011). Seedlings of *Posidonia oceanica* showed reduced growth rates, lower leaf formation rates and lower leaf biomass per shoot after 3 months of exposure to temperatures encompassing those projected for the Mediterranean Sea during the 21st century (Olsen et al. 2012). However, thermal stress coincides with increases in flowering intensity in *P. oceanica* of the Mediterranean (Diaz-Almela et al. 2007), so the timing of a thermal event could determine effects on population dynamics. Furthermore, response to warming can be delayed, such that reduced growth occurs after the warming event (Reynolds et al. 2016), which may be further indication of metabolic imbalances resulting from the thermal stress.

### 21.3.3 Thermal Optima

Seagrass thermal optima can be defined in a number of ways, including: photosystem II efficiency, photosynthetic rates (carbon fixation), net productivity, compensation irradiance, seasonal variation in growth and distributions with the optima declining across this range of parameters (Lee et al. 2007). Thermal optima are also species specific and tend to reflect distributional ranges such that tropical species have higher thermal optima than temperate species (Campbell et al. 2006; Lee et al. 2007; Collier et al. 2011; 2017). When based on photosystem II efficiency, thermal optima reach 40 °C in tropical seagrasses (Campbell et al. 2006), and 30 °C for temperate-acclimated species (Ralph 1998). However, due to respiratory carbon loss, thermal optima for net productivity of leaves is lower reaching 27.0–35.0 °C in tropical species (Lee et al. 2007; Collier et al. 2011, 2017; Pedersen et al. 2016) and 27–32.5 °C for temperate species (Lee et al. 2007; York et al. 2013). There is less information on optimum temperature for growth because it can be harder to measure. Furthermore there are many different factors that can affect optimal growth temperature because it involves a complex range of processes (Lee et al. 2007). In *Posidonia oceanica* from the Mediterranean, the optimum temperature for growth is more than 15 °C lower than for photosynthesis (Lee et al. 2007). In *Halophila ovalis*, which has a low proportion of below-ground biomass contributing to respiratory loss, the difference is much smaller dropping from 27.5 to 25 °C. In some cases the differences can be marginal or even reversed but there are few available data comparing them for most species (Lee et al. 2007). However, the determination of optimal growth temperatures from seasonal data may be confounded by changes in incoming irradiance, as light does affect thermal optima.

There are a number of factors that can affect thermal optima. Increasing light availability can allow seagrass to withstand high temperatures, thus raising their thermal optima (Bulthuis 1983; Collier et al. 2011; Collier et al. in prep). Therefore, in summer or under warmer conditions, they may become more vulnerable to low light conditions than when ambient water temperature is cooler (Hillman et al. 1995; Collier et al. 2016). Furthermore, the allocation of biomass to below-ground biomass can also affect thermal optima such that higher allocation to below-ground biomass reduces thermal optima of net productivity (Collier et al. 2017). A large range in the thermal optima for photosynthesis in *Z. marina* across latitudinal gradients suggest that seagrasses can acclimate to ambient water conditions. However, there was limited seasonal acclimation in the thermal optima of photosynthesis in *Zostera marina* increasing by 2 °C over seasonal water temperature change when ambient water temperature ranged from 3 to 22 °C (Staehr and Borum 2011). Plants that performed the best at optimum temperatures did not perform as well at high temperatures and therefore genetic diversity improves chances of surviving events (Reynolds et al. 2016).

In *H. uninervis* and *C. serrulata*, there was limited acclimation (0–1.2 °C) over 1500 km from the northern Great Barrier Reef to Moreton Bay and between summer and winter at Moreton Bay, where ambient temperature ranged from 21.0 to 28.8 °C across latitudes and seasons (Collier et al. 2017). Due to limited on-site acclimation and rising in situ temperatures meadows already living close to their thermal optima are at risk from thermal stress in the future, Pedersen et al. (2016), and catastrophic climate-related loss has already occurred.

### *21.3.4 Range Shifts*

Climate change is predicted to alter geographic distributions as species are forced to shift their ranges when physiological tolerances are exceeded, as has been recorded for temperate macroalgae along the Australian Pacific and Indian Ocean coastlines (Wernberg et al. 2011, in press).

Increased rates of shoot mortality and limited recruitment of new shoots that are more sensitive to warming (e.g. Olsen et al. 2012) may ultimately affect the distribution of seagrasses and lead to local extinction or displacement of species that grow at the edge of their thermal tolerance (Short and Neckles 1999). Populations living near their range limit are highly vulnerable. For example, in Shark Bay, Western Australia, there was catastrophic dieback of the seagrass *Amphibolis antarctica*, which was growing near its low-latitude range limit, following a heat wave in 2010/11 (Fraser et al. 2014; Thomson et al. 2015) (see Sect. 5.1). However, even populations well within their thermal range may be adversely affected and there may be local extinction or reduced abundance following extreme events. For example, in a relatively un-impacted (anthropogenic impacts) area of Spencer Gulf in South Australia, severe dieback of 8269 ha of seagrass (*Amphibolis antarctica* and *Zostera* spp.) primarily in shallow and intertidal habitat was attributed to an El Niño event in 1993. A further example for event-driven loss is for *Posidonia oceanica* from the Mediterranean where average mean annual water temperature in 2002–2006 was 1 °C above the long-term average (1988–1999) driven by 2 heat waves led to shoot mortality ranged from 7 to 12% year$^{-1}$ (Màrba and Duarte 2010).

### *21.3.5 Temperature and Resilience*

Genetic diversity and acclimation may provide some buffer for warming and heatwaves. Genotypes that performed best (faster growth) under normal conditions suffer the most from warming, thus as conditions return to normal you may get individuals that do not perform as well more dominant (Reynolds et al. 2016). However, experimentally manipulated genotypic diversity did not increase tolerance to warming in *Z. marina* (Ehlers et al. 2008). Genetic diversity of *Z. marina* increased biomass production and density during a near-lethal thermal event in the Baltic Sea. Furthermore, some populations have higher tolerance to extreme temperatures. For example, *Z. muelleri* from Gladstone in the southern Great Barrier Reef was highly sensitive (negative net production, almost complete mortality after 4 weeks) to 33 °C (Collier et al. 2011) and *Z. muelleri* from lake Macquarie in NSW suffered complete mortality after 40 days exposure to 32 °C. In contrast, *Z. muelleri* from Midge Point in the central Great Barrier Reef was more heat tolerant and was able to maintain positive net productivity and vigorously growing shoots after seven weeks of continued exposure to 35 °C while it increased its thermal optima to 37.3 °C (Collier et al. in prep). Maintaining genetically diverse populations and identifying more heat tolerant individuals may provide an active management option to combat warming and range shifts.

## 21.4 Combined Effects of Warming and OA

The rise in atmospheric $CO_2$ will create conditions of increasing temperatures and OA in concert. These two factors should therefore be considered together, particularly as they fundamentally influence biochemistry and physiology of plants. The combined effects of warming and OA on seagrasses and other aquatic producers are not well understood and studies looking at interactions are lacking (Fig. 21.6). In the terrestrial literature, elevated $[CO_{2(aq)}]$ partially compensates for deleterious effects of elevated temperatures and raises temperature optima. It is possible similar effects will be seen in macrophytes. Three seagrass species exposure to elevated $pCO_2$ (up to 1949 μatm) across a range of temperatures between 21 and 35 °C for seven weeks showed varying responses (Collier et al. in prep). Maximum productivity was increased at the highest $pCO_2$ across all temperatures for *Zostera muelleri*, but had little effect on *Cymodocea serrulata* and *Halodule uninervis* at temperatures up to 30 °C. There was a sharp decline in productivity, growth and shoot density of *C. serrulata* and *H. uninervis* at 35 °C, which was exacerbated by high $pCO_2$. For some species, it therefore appears that combined warming and OA may reduce seagrass productivity and OA may compound response to future extreme heat events. It is clear that while there are numerous studies on the effects of warming on seagrasses and we are beginning to understand the possible range of responses of seagrasses to OA, we have a very limited understanding of the

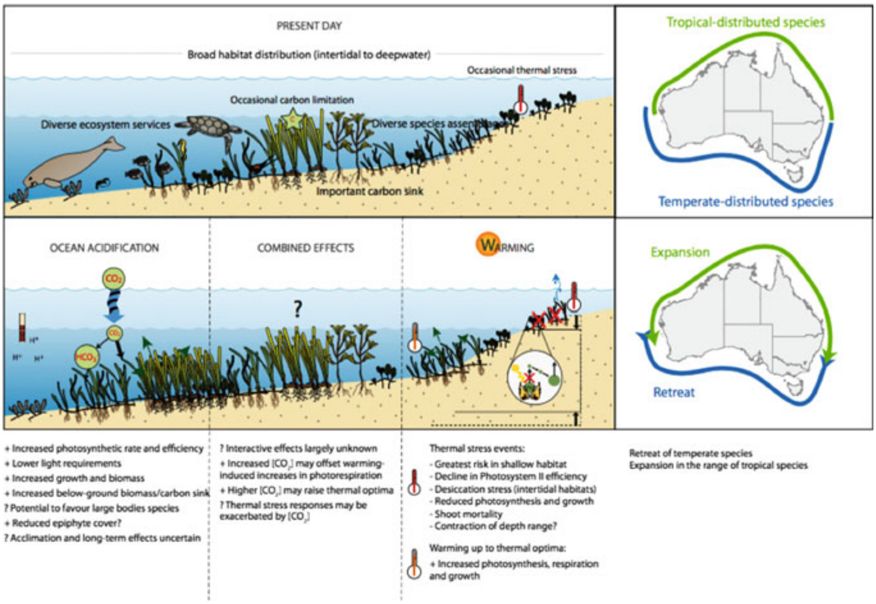


**Fig. 21.6** Seagrass meadows and future effects of OA and warming. The top panel shows present-day seagrasses made up of diverse species assemblages, which are occasionally C-limited and thermally stressed, but that provide diverse ecosystem services. The current distributions of temperate and tropical species around Australia are shown (top right). In the bottom panel the effects of ocean acidification, warming and the combined effects are illustrated. Ocean acidification is predicted to have mainly positive effects on seagrasses (+) wheras thermal stress will have negative impacts (−). The combined effects are largely unknown (?). In Australia, tropical species are predicted to extend their range, while temperate species may retract in the future (bottom right panel)

interactions of these two processes. Results thus far have shown species-specific differences in responses and that $CO_2$ can raise thermal optima or exacerbate thermal stress (Fig. 21.6).

## 21.5 Interactions with Other Stressors

As atmospheric $pCO_2$ increases, marine ecosystems will experience the combined effects of OA and warming, but climate-change is also associated with many concurrent shifts, e.g. ocean circulation, stratification, precipitation and runoff, nutrient concentrations and oxygen content that will have profound biological effects (e.g. Doney et al. 2012). In addition, the effects of anthropogenic $CO_2$ emissions do not act in isolation, but must be considered together with current stressors including widespread coastal eutrophication (Burkholder et al. 2007), hypoxia (Diaz and Rosenberg 2008), overfishing (Jackson et al. 2001) and turbidity

(Erftemeijer and Lewis 2006) to mention a few. The combined effect of multiple stressors generally is greater than the sum of individual stressors (Darling and Côté 2008). Multiple stressors are particularly concerning for management as combined effects are difficult to predict, yet have the potential to erode resilience and lower the threshold for sudden phase shifts in ecosystems (Harley et al. 2006; Hawkins et al. 2008). Foundation species, like seagrasses, have a disproportionately large influence on the ecosystems they grow in and support other species and ecosystem processes (Ellison et al. 2005) and their loss can lead to impacts that permeate through the trophic structure of the ecosystem.

### *21.5.1 Warming, Runoff and Anoxia—A Case Study of Shark Bay*

Shark Bay is a World Heritage listed marine embayment on the west coast of Australia where one of the recognised key environmental values are the large extensive seagrass meadows that support high marine biodiversity, including significant populations of dugongs, turtles, and tiger sharks (Kendrick et al. 2012). Biodiversity is high in Shark Bay as it overlaps the temperate and tropical biomes, and contains a range of tropical and temperate marine species existing near the limit of their thermal tolerance. For example, Shark Bay contains 12 species of temperate and tropical seagrasses (Walker et al. 1988). The Australian endemic seagrass *Amphibolis antarctica* is the dominant primary producer in Shark Bay, covering approximately 3700 km$^2$ ($\sim$85% of seagrass covered area) of Shark Bay (Walker et al. 1988).

In the austral summer of 2010–2011, a marine heat wave coined the Ningaloo Niño (Feng et al. 2013) drove water temperatures 2–4 °C higher than normal summer temperatures for many weeks along the west coast of Australia, resulting in large mortalities and phase shifts in marine communities (see Wernberg et al. 2013, in press). In Shark Bay, defoliation was observed in *Amphibolis antarctica* across the whole bay in response to high temperatures, with areas of extreme defoliation occurring in association with river plumes from floods in the eastern Faure Sill and Hamelin Pool region (Fraser et al. 2014) and in deeper waters where light was limiting (Thomson et al. 2015).

The heatwave and flood event led to two responses in *A. antarctica*—a short term, highly visible reduction in leaf biomass; and a long term, less visible reduction in belowground biomass (Fraser et al. 2014). Loss continued subsequently and large areas of *Amphibolis* meadows disappeared in the locations where defoliation was the greatest. It was inferred that much of the subsequent loss in seagrasses was driven by a combined high biological oxygen demand from bacterial breakdown of the large pulse of leaf material into the system and low rates of seagrass recruitment from flowering and seed abortion (Sinclair et al. 2016). In some areas of the bay, the deoxygenated waters were observed as turbid black water (Fraser, pers obs).

Loss in seagrass cover has persisted for six years, and led to changes in the trophic structure, where grazing of seagrasses by tropical fish species has increased (Kendrick pers. obs.). Also, green turtle health has declined through starvation and their behaviour in relation to higher order carnivores like tiger sharks has become riskier (Thomson et al. 2015). Rising sea temperature (in this case associated with an abnormal event) was the proximate cause of seagrass defoliation, but additive effects of high light attenuation from floods and higher detrital loads, subsequent bacteria activity and elevated oxygen demand, along with modified and more focussed herbivory has ultimately driven a single event to an ecosystem-wide phase shift that has persisted for more than 6 years. Ultimately, the loss of the temperate seagrass *Amphibolis antarctica* over a potential 100,000 ha from their original distribution in Shark Bay (extrapolated from loss of biomass and cover from quadrats in Fraser et al. 2014; Thomson et al. 2015) has consequences to ecosystem resilience and will increase susceptibility of seagrasses ecosystems in Shark Bay to episodic events like marine heatwaves that are predicted to increase with climate change.

### 21.5.2 $CO_2$ and Nutrient Availability

Nutrient availability can influence the outcomes of $CO_2$ enrichment for plants. The importance of nutrient enrichment in regulating productivity responses to $CO_2$ enrichment have been observed in terrestrial plants (Stitt and Krapp 1999) and marine macroalgae (Gordillo et al. 2003; Hofmann et al. 2014; Russell et al. 2009). This is because many processes in carbon metabolism, such as photosynthesis and formation of organic acids and starch (Scheible et al. 1997), rely on nutrient availability (Touchette and Burkholder 2007). Ocean acidification has been shown to increase the leaf tissue carbon-to-nitrogen (C:N) ratios in seagrasses (Jiang et al. 2010; Campbell and Fourqurean 2013a; Alexandre et al. 2012), which suggests that $CO_2$ enriched plants are nitrogen limited (Udy et al. 1999; Mellors et al. 2005). While it is speculated that moderate increases in nutrient availability may enhance ocean acidification responses in seagrasses (Palacios and Zimmerman 2007; Apostolaki et al. 2014), experimental work on the interactive effects of ocean acidification and nutrient enrichment is limited.

Combined $CO_2$ and nitrate enrichment, at levels approximating present day flood plumes at the Great Barrier Reef (Devlin et al. 2011), did not boost net photosynthesis and growth in *Halodule uninervis* or *Thalassia hemprichii* (Ow et al. 2016a). Furthermore, $CO_2$ enrichment did not increase nitrogen demand in either species, as there was no change in nitrate uptake or assimilation rates with elevated $CO_2$. It is possible that the lack of a response was related to the strong dependence of seagrass on light levels, which averaged 9 mol $m^{-2}$ $d^{-1}$ in the study, lower than the 15–20 mol $m^{-2}$ $d^{-1}$ typically measured in north Queensland shallow seagrass meadows (McKenzie et al. 2015).

$CO_2$ enrichment may not always create nutrient limitation in seagrasses. Nitrogen-use efficiency in seagrasses can be improved, e.g. through nitrogen recycling or re-allocation within the plant (Romero et al. 2006). At natural $CO_2$ seeps, no difference in tissue nutrients were found between seagrasses growing in $CO_2$-enriched waters around the seeps compared to seagrasses growing away from the seeps at normal pH, suggesting $CO_2$-induced nitrogen limitation was absent (Takahashi et al. 2015). Hence, seagrasses might not necessarily require nutrient enrichment to benefit from ocean acidification.

Growth of other marine macrophytes, such as phytoplankton and seagrass epiphytes, is also enhanced by ocean acidification and nutrient enrichment. These marine macrophytes compete for the same resources (light, nutrients and dissolved inorganic carbon) with seagrasses (Drake et al. 2003). Campbell and Fourqurean (2014) documented changes in epiphytic composition during exposure to increased $CO_2$ levels and nutrient enrichment. A reduction in coralline algae and an increase in turf algae resulted from $CO_2$ enrichment (2.6× ambient $CO_{2(aq)}$). While Campbell and Fourqurean (2014) concluded that ocean acidification can outweigh the influence of nutrient addition on seagrass epiphytes, how these compositional changes might affect seagrass production were unquantified. Moderate nutrient enrichment could possibly augment $CO_2$ responses in nutrient-limited plants, bringing enhanced productivity while preventing nutrient imbalance in leaf tissue (Agawin et al. 1996; Mellors 2003; Udy et al. 1999; Stitt and Krapp 1999). On the other hand, strong and sustained nutrient enrichment under ocean acidification may indirectly limit seagrass responses by altering the cover and composition of competing epiphytic and drift algae (Koch et al. 2013; Burkholder et al. 2007) and may challenge the predicted advantages to seagrass productivity under ocean acidification.

### *21.5.3 $CO_2$ and Light Limitation*

Seagrasses have high light requirements and a decrease in light availability, e.g. due to sedimentation and turbidity, reduces the potential for photosynthesis and carbon acquisition (Touchette and Burkholder 2000). When photosynthesis is light-limited, the demand for dissolved inorganic carbon may be reduced (Durako and Hall 1992) and hence, affect the way seagrasses respond to ocean acidification. Seagrasses growing under low irradiance may show a diminished response to OA. For example, in light-limited *Zostera marina*, the increase in shoot production and biomass with $CO_2$ enrichment were much diminished compared to those of light-replete plants (Palacios and Zimmerman 2007). Conversely, light limitation may increase the dependence on $CO_{2(aq)}$ concentrations because the use of $HCO_3^-$ as photosynthetic substrate is energetically costly (Mercado et al. 2003; Schwarz et al. 2000). Various studies have shown that low light adapted seagrasses may benefit more from ocean acidification ($CO_{2(aq)}$ enrichment). The shade-morphotype of *Zostera noltii* and deep-water (10–12 m) *Halophila ovalis* and *Cymodocea serrulata* exhibited greater increases in photosynthesis (measured as oxygen evolution or relative electron transport rates) compared to their shallower intertidal counterparts when subjected to an increase in DIC concentration (Schwarz et al. 2000; Mercado et al. 2003). Similarly in Ow et al. (2016b), a larger increase in photosynthetic capacity ($P_{max}$) from $CO_{2(aq)}$ enrichment was observed in *C. serrulata* growing in low light (average 35–100 μmol $m^{-2}$ $s^{-1}$ PAR) than those growing in saturating light (average 380 μmol $m^{-2}$ $s^{-1}$ PAR). Seagrass species growing at low irradiances tend to exhibit a lower capacity to use $HCO_3^-$ and a higher reliance on $CO_{2(aq)}$ (Mercado et al. 2003; Ow et al. 2016b), suggesting that they can benefit more from ocean acidification.

Light attenuation can limit epiphytic growth, freeing up competition (Drake et al. 2003) and thus indirectly enhancing OA responses in seagrasses. $CO_2$ enrichment had positive effects on growth and biomass of an Australian species, *Amphibolis antarctica*, in low light treatments (43 μmol $m^{-2}$ $s^{-1}$ PAR) (Burnell et al. 2014b). Conversely, in high light (167 μmol $m^{-2}$ $s^{-1}$ PAR), the overgrowth of seagrass with filamentous algal epiphytes caused growth and biomass to decrease with elevated $CO_2$. In a sedimentation event, fine sediment particles may be caught in the epiphytic matrix on seagrass leaf blades. The resulting sediment "coat" could smother live seagrass surface by cutting off light, $CO_2$ and nutrients. Even though seagrasses growing under low light levels may benefit more from $CO_2$ enrichment, a strong and sustained light reduction might still outweigh $CO_2$ enrichment effects on seagrass productivity (Ow et al. 2016b; Zou and Gao 2009; Palacios and Zimmerman 2007). Despite the increase in $CO_{2(aq)}$, $HCO_3^-$ remains the largest pool of DIC substrate and growing in low irradiance would render $HCO_3^-$ use costly, and prevent seagrasses from maximizing their photosynthetic potential. Species whose growth responses appear to depend more on light availability than DIC concentration, e.g. *H. uninervis* (Ow et al. 2016b) and *Z. marina* (Palacios and Zimmerman 2007), might be more vulnerable to sedimentation and turbidity events.

## 21.6 Conclusions

Seagrasses have been described as winners in the future ocean as they are predicted to increase productivity and growth under OA. There is clear evidence that warming and increased $pCO_2$ will have substantial effects on seagrass metabolism, growth, species interactions and future distributions, but many questions remain about how the combined effects will shape future seagrass meadows. We know little about how interactions with other stressors will affect seagrasses and it is difficult to predict how aggregated ecosystem functions will be affected, including the ability of seagrass meadows to continue to perform ecosystem services. High rates of productivity are central to many of the ecosystem services that seagrasses provide, e.g. a food source for fish, invertebrates, dugongs, sirenians and turtles, habitat for commercially important fishery species, a coastal filter for nutrients and sediments and stabilizer of the substrate.

Seagrass meadows sequester carbon into a long-term carbon sink as the matrix of roots and rhizomes and the organic matter trapped within can be buried for centuries to millennia (e.g. Romero et al. 1994 and Chap. 22). Seagrass meadows make up a globally significant carbon stock (between 4.2 and 8.4 Pg carbon) and are estimated to capture around 27.4 Tg C $\text{year}^{-1}$ (Fourqurean et al. 2012). Global fossil-fuel emissions of $CO_2$ add approximately 9400 Tg C $\text{year}^{-1}$ to the atmosphere (Boden et al. 2015). Seagrasses therefore capture <0.3% of emissions globally. While this represents a relatively small effect, it is equivalent to 10% of the total carbon capture capacity of the ocean (Sabine et al. 2004; Irving et al. 2011). In a future high-$CO_2$ ocean seagrass carbon capture could be enhanced if growth and productivity increase and the allocation of biomass to belowground tissues increases (e.g. Russell et al. 2013). Large-scale restoration of seagrass meadows has been suggested as a way of improving global carbon storage, however, this approach is unlikely to substantially improve carbon capture unless restoration efforts are undertaken on an industrial scale (Irving et al. 2011). Every effort should be made to protect and conserve seagrass habitats as present rates of seagrass loss may result in the release of almost 300 Tg C annually (Fourqurean et al. 2012).

Despite a recent increase in climate-change research in marine systems, we lack understanding of how whole ecosystems, including seagrass meadows, are going to respond to warming and OA. Knowledge gaps exist all the way from basic biochemical stress responses, to growth, biomass allocation, reproductive output, range shifts to community and ecosystem level responses. It is particularly difficult to predict longer-term responses and possible adaptation to combined warming and OA.

Research gaps

1. The individual effects of warming and OA have only been examined for a limited number of seagrass species. This is a particular issue for Australia being a diversity hotspot with multi-species seagrass meadows.
2. As this review has demonstrated, there is a lack of studies examining combined effects of OA and warming. The limited information we have suggests that there may be large differences among species and that outcomes of $CO_2$ enrichment can even be negative at high temperatures.
3. There is a need to conduct longer-term studies to identify adaptation to climate change. Genetic diversity and its role in resilience of seagrasses to climate change should also be considered. We should aim to determine how we could manage seagrass resources to maximize resilience to climate change.

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# Chapter 22
# Estimating Seagrass Blue Carbon and Policy Implications: The Australian Perspective

**Peter J. Ralph, J. R. Crosswell, T. Cannard and Andrew D. L. Steven**

**Abstract** Blue carbon policy supports carbon sequestration whilst also conserving our remaining seagrass meadows. The complex biogeochemical processes within the sediment of seagrass meadows are responsible for the longevity of the stored carbon. Carbon stock and accumulation rates are controlled by the interaction of hydrodynamic, geochemical and biotic processes unique to each meadow. Carbon content (stock and flux) of a meadow must be quantified for inclusion in carbon accounting, whether for market trading or national greenhouse gas accounting. Management of seagrass blue carbon also requires estimates of additionality, leakage, permanence, conversion and emission factors.

## 22.1 What Is Blue Carbon?

Blue carbon is carbon that has been captured and sequestered by coastal marine vegetated habitats, which include seagrass meadows, mangrove forests and salt marshes. These habitats can be highly productive and have been identified as strong carbon sinks, as some seagrass species and regions support remarkably high carbon

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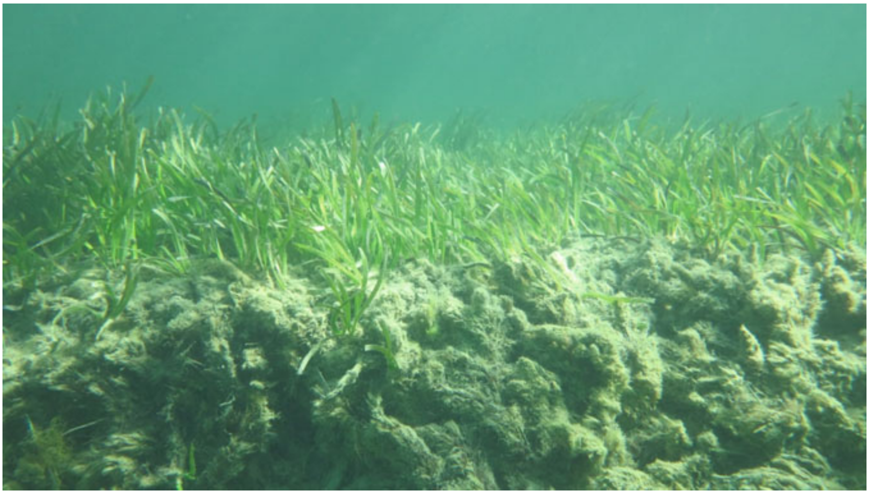

**Fig. 22.1** *Posidonia* escarpment in Shark Bay, Western Australia, with living plants at the surface, and a deep layer of organic-rich sediment underneath, exposed by erosional processes. Photograph by Paul Lavery (ECU)

burial rates. Blue carbon can be stored for millennia, unlike terrestrial “green” carbon which turns over more rapidly through cycles of plant growth and decay. In blue carbon habitats, particularly seagrass, most of the carbon is stored in below-ground biomass (Fig. 22.1) and in anoxic sediment where microbial decomposition of litter (or remineralisation) is extremely slow (Enríquez et al. 1993). These low decomposition rates, combined with high primary productivity, allow blue carbon habitats to build up large, persistent carbon stocks.

Biogeochemical cycles of seagrass meadows have been studied for the past few decades. However, there has been a resurgence in seagrass research driven by the recent connection between long-term carbon storage in seagrass meadows and efficiency of this carbon for natural sequestration (e.g. McLeod et al. 2011; Duarte et al. 2010, 2011; Kennedy et al. 2010). This recent research has led to a better understanding of the biogeochemical mechanisms, magnitudes, and uncertainties associated with carbon capture in blue carbon habitats.

## 22.2 Seagrass Drive Natural Carbon Sequestration

Seagrass are responsible for about 15% of the total carbon stored in the ocean, although they represent less than 0.2% of the total area of the ocean (Garrard and Beaumont 2014). Seagrass sequester up to 35 times more carbon per area into long-term storage as compared to tropical forests (McLeod et al. 2011). Unfortunately, coastal marine habitats are some of the most threatened ecosystems on Earth. These habitats are being degraded at a rate that is equivalent to four times that of tropical forests, and climate change continues to exacerbate this situation. Since the 1980s, the global rate of seagrass loss is 7% per year (Waycott et al. 2009) and losses are even greater in some areas of Australia's increasingly urbanised coastline. For example, around half of the seagrass meadows in New South Wales have been lost relative to their historical coverage (Zann 2000). Apart from reducing potential carbon storage, the loss of seagrass also degrades an extensive range of other ecosystem services (including storm protection, maintaining coastal water quality and supporting coastal fisheries). The value of these services continues to increase given their role as a buffer against impacts of global climate change. Seagrass meadows also have the ability to bolster long-term coastal geomorphological resilience through erosion management and wave energy reduction (Arkema et al. 2013; Grimsditch et al. 2013), and potentially, mitigation from sea level rise (Orth et al. 2006). Therefore, these critical habitats need to be protected in order to safeguard carbon stores and ensure their ongoing ecological function and thereby maintain their associated highly valued ecosystem services.

## 22.3 Overview of Carbon Biogeochemistry in Seagrass Meadows

Healthy seagrass meadows require good water quality, including suitable levels of nutrients, sufficient light and stable sediments to maintain productive meadows. Loss of seagrass meadows can be triggered by acute disturbances or through chronic impacts of climate change and anthropogenic modification to coastal ecosystems (Barbier et al. 2011). Direct removal of seagrasses can occur during coastal development activities such as dredging or boat moorings. Indirect effects of human activity on seagrass occur through reduced water quality, such as eutrophication (nutrient pollution), and episodic sediment plumes from catchment runoff, which reduce light and smother the plants.

Carbon stocks and accumulation rates in seagrass meadows are controlled by a range of factors (Fig. 22.3). Accumulation rates depend on environmental characteristics of the meadow, such as water depth and velocity, as well as the physical characteristics of the seagrass (Serrano et al. 2014). Different species of seagrass accumulate carbon at different rates in relation to their growth form, compositional makeup of tissues (recalcitrance) and sediment type (Lavery et al. 2013; Trevathan-Tackett et al. 2017). Understanding the hydrodynamics of a site will improve estimates of local carbon accumulation and stocks. However, accumulation rates can also be influenced by other abiotic factors, including sediment grain size and sediment type (terrigenous or calcareous). It is more difficult to monitor and establish causality between these indirect relationships.

Blue carbon stored in seagrass meadows is classified as either autochthonous or allochthonous depending on its source. Autochthonous carbon is carbon that has been biologically fixed within the seagrass meadow, but was previously dissolved in the water column (Fig. 22.3). Allochthonous carbon is carbon that was biologically fixed in connected environments, but has been hydrologically transported to and deposited in the seagrass meadow. It has been estimated that up to 50% of the carbon within a seagrass meadow is autochthonous and 50% allochthonous. Seagrass have a burial efficiency of up to 10% of the fixed carbon that is stored within the plant, whereas other marine plants, such as pelagic phytoplankton, have burial rates of about 0.5%. Burial efficiency in seagrass meadows can vary depending on several biological factors, including bioturbation, bacterial diversity and the degradation rate of autochthonous and allochthonous carbon types (Mateo et al. 2006).

## 22.4 Australian Seagrass Blue Carbon Habitats

Australia has an extensive marine area which contains a significant fraction of all global vegetated coastal ecosystems. Lavery et al. (2013) estimated Australian seagrasses to contain 155 Mt of carbon; given a diverse range of species-specific $C_{org}$ storage rates to a depth of 25 cm (for comparison Ajani and Comisari 2014 used 100 cm depth). For example, it has been estimated that 1–2% of all global seagrass carbon stocks are contained within Shark Bay alone due to its large area of seagrass meadows and high accumulation rates. However, carbon stocks vary across Australia's 9,256,900 hectares of seagrass meadows (Lavery et al. 2013). Current Australian datasets show a large range in sediment organic carbon content, ranging from 1.09 to 20.14 mg $C_{org}$ $cm^{-3}$ (Lavery et al. 2013; Serrano et al. 2014). Smaller stature seagrass species generally have lower organic carbon stocks, but they can also cover a large area of the tropical northern coastline; they are estimated to account for 46% of Australia's seagrass carbon. The remaining 54% is thought to be mostly stored in large-stature, meadow-forming temperate species such as *Posidonia* and *Amphibolis.*

### *22.4.1 How Is the Carbon Budget Estimated at a Seagrass Site?*

To build a carbon budget, three characteristics of the meadow must be determined: the area of the meadow, an estimate of the carbon stored in the sediment and the rate that the sediment is accreting or eroding. This process to build a carbon budget is described in more detail below:

1. *Map site boundaries and assess heterogeneity using satellite remote sensing or aerial photos.* Estimating boundaries can be complex due to water depth or tidal variation when observing sparse intertidal species. Satellite remote sensing

provides a synoptic view of a sufficiently wide area to provide national estimates of seagrass coverage, but may not have the resolution for regional estimates. Remote sensing can also be used to routinely confirm the extent of the managed seagrass meadows over time, especially when linked to a carbon financing scheme. Historical aerial photos and satellite remote sensing can also be used to identify lost, degraded or converted meadows, as well as the effectiveness of restoration or habitat recovery.

2. *Quantify carbon inputs from other habitats*. Riverine particulate organic carbon (POC) and oceanic phytoplankton, zooplankton and detritus are typically the main sources of allochthonous carbon moving into a meadow. If there is significant input from other nearby blue carbon habitats, or if there are multiple riverine inputs, then stable isotopes, molecular tracers and elemental ratios can be used to determine carbon sources. Partitioning allochthonous carbon sources ensures that carbon uptake/release is not double counted for multiple ecosystems.
3. *Quantify metabolism of the site*. If possible, it is useful to quantify seagrass photosynthesis, seagrass respiration and microbial respiration, as this assists in estimating autochthonous input.
4. *Estimate carbon stocks and fluxes*. Carbon concentrations can vary with depth; sediment cores provide a vertical profile that considerably improves stock estimates. Radio-isotopes can be used to determine the age of carbon down the sediment profile and accretion rates can be estimated based on the change in carbon concentration over time. In highly productive and heterogeneous habitats, gas fluxes between the sediment, water and air may also need to be quantified in order to determine ecosystem metabolism over shorter timescales (Macreadie et al. 2014).

Finally, once the areal extent is determined (and regularly measured to identify changes), we can estimate the value of the blue carbon resource by scaling a limited number of stock (and flux) estimates to cover the area under management control.

## 22.5 Blue Carbon Markets

Blue carbon financing offers a mechanism to protect and capitalise on other ecosystem services provided by coastal marine vegetated habitats. In developing policy to support blue carbon markets, there is an opportunity to incentivise the promotion of healthy coastal marine vegetated habitats, as well as blue carbon storage and production. In Australia, it is no coincidence that significant areas of seagrass meadows are situated in regions that exhibit outstanding universal values (OUV) and are recognised in World Heritage listings, e.g. Great Barrier Reef, Shark Bay, Ningaloo coast, and the Great Sandy Straits. Accordingly, economic non-market values have been revised from $13,786 per hectare in 1997 to $193,843 per hectare in 2016 (Pendleton et al. 2016). The increases in estimated value have arisen as now more of the thirteen components of total economic value for coastal wetlands have been monetised (Costanza et al. 1997; Pendleton et al. 2016). The development of robust and rigorous non-market estimates will be further hastened with a deeper understanding of seagrass carbon stocks and flows.

The Blue Carbon Initiative and the Blueprint for Ocean and Coastal Sustainability are both international programs calling for protection, and restoration of carbon-rich coastal and ocean habitats. These programs also call for the development of global blue carbon markets (Lau 2013; Ullman et al. 2013; IOC/UNESCO 2011; Conservation International 2015). Quantifying coastal carbon stocks found in mangroves, saltmarsh and seagrass is a vital step toward establishing this market (Fig. 22.2), but there remain several obstacles. For example, the transient nature of seagrass meadows (fluctuate seasonally and spatially), poses particular challenges for monitoring coverage and assessing the permanence of carbon stocks. Accordingly, understanding boundaries and carbon fluxes for each blue carbon habitat are crucial factors required for both policy and market development.

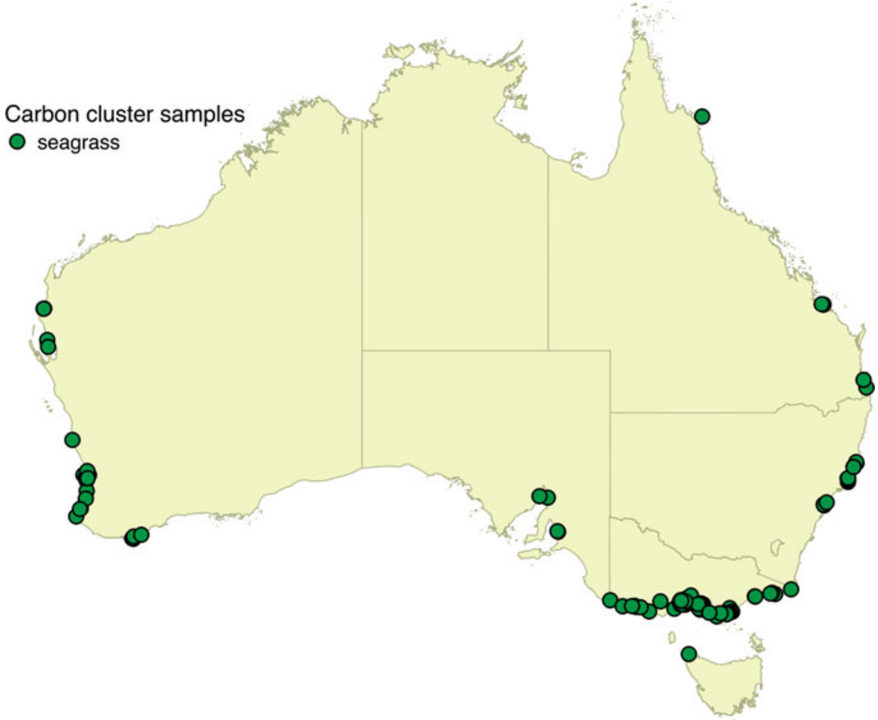

**Fig. 22.2** Map showing the distribution of sediment cores collected at Australian sites to estimate seagrass C stock

## 22.6 International Policy and the Impact on Australia

In the 2006 IPCC Guidelines for National Greenhouse Gas inventories, seagrass were not mentioned. Without direct recognition of seagrass as a blue carbon habitat in IPCC guidelines, there have been no incentives for carbon financing, conservation of carbon stocks, or the restoration of meadows.

In 2009, UNEP published a report entitled "Blue Carbon: A rapid response assessment" (Nellemann et al. 2009) which described how seagrass were a critical component of blue carbon coastal vegetation. This report was the catalyst for the inclusion of blue carbon into the IPCC, NGOs and intergovernmental policy advisors. It also provided a list of key recommendations to ensure blue carbon protocols were developed. This triggered the establishment of the Blue Carbon Initiative which comprised two working groups: scientific and policy. The Blue Carbon Initiative (CI, IUCN, UNESCO-IOC) has been driving the evolution of both policy and the underlying science to allow blue carbon habitats to be incorporated into national greenhouse gas inventories, and to enable blue carbon trading on carbon markets. At the international level, policy frameworks are being developed to improve the management of these vulnerable coastal habitats and to create financial and other incentives to conserve, restore and sustainably use these ecosystems (Pendleton et al. 2016).

In 2013, a Wetlands Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas inventories was adopted which included coastal wetlands, specifically seagrasses, mangroves and salt marshes. Methodologies for coastal wetlands require approval from UNFCCC for inclusion in IPCC reporting. There are three tiers of assessment in IPCC reporting: Tier 1—national estimates based on a global database; Tier 2—national estimates based on regional/country-based data; and Tier 3—estimates from high-resolution observations and models repeated over time. Nationally relevant data is essential to develop Tier 2 estimates, and ultimately, Tier 3 requires habitat-specific estimates. In order to adopt the 2013 Wetlands Supplement, habitat-specific emission factors and sequestration rates are required to calculate both stocks and fluxes. Indeed, the Wetlands supplement triggered much of the research required to support policy development for the inclusion of seagrass in national carbon accounting. Similarly, Reduce greenhouse gas Emissions from Deforestation and forest Degradation (REDD) was established under the United Nations Framework for Climate Change Convention (UNFCCC). Of note, Luisetti et al. (2013) calculated that the removal of incentivised approaches such as REDD could result in extensive loss of blue carbon ecosystems and associated economic value losses as high as US$1 billion by 2060.

The current EU carbon stock accounting framework draws heavily on the System of Environmental-Economic Accounting (SEEA) Central Framework and the System of National Accounts (SNA) and enacts the principle of completeness or comprehensiveness (Lau 2013; Ullman et al. 2013; IOC/UNESCO 2011). Furthermore, the definition, classification, scope and valuation of environmental assets, contained in the Australian Environmental-Economic Accounts (AEEA), is defined by the aforementioned SEEA Central Framework.

## 22.7 Development of an Australian Blue Carbon Policy for Seagrass

A Blue Carbon policy must address several complex issues to ensure it is consistent with other IPCC-based mitigation strategies (Ullman et al. 2013). The terms described below have been developed for forest-based mitigation and have been translated into blue carbon habitats. Values for each terms are required for national carbon accounting, as well as market evaluation. Australia is yet to release an integrated blue carbon strategy and policy to mitigate climate change. Much of the necessary groundwork has been completed over the past three years as part of the CSIRO Marine and Coastal Carbon Biogeochemistry Cluster (including Trevathan-Tackett et al. 2015; Rozaimi et al. 2016). The following issues need to be examined by the UNFCCC in support of carbon accounting: ***emission factors, additionality, leakage, permanence*** and ***conversion*** (defined below). These issues are also the main elements in "net flow accounting" which avoids double-counting the amount of converted carbon, but would recognise carbon loss due to leakage and conversions (ABS 2015).

When a seagrass meadow is degraded or destroyed, the sediment organic carbon can be remineralised to inorganic carbon. Depending on water chemistry, some of this inorganic carbon can be emitted to the atmosphere as $CO_2$. The portion of the original amount of organic carbon stock that is remineralised and subsequently lost to the atmosphere is called the "**emission factor**" (Fig. 22.3). For example, Cebrian (2002) estimated that the loss of mangroves around the globe has released $3.9 \times 10^8$ tonnes C into the atmosphere from long-term blue carbon stocks. Establishing emission factors for Australian seagrass will require development of new carbon accounting protocols. These new protocols must be able to quantify how much seagrass carbon is lost to the atmosphere when a habitat is degraded/destroyed, and how much carbon is redistributed to another oceanic carbon stock. Historical evidence of lost meadows can provide an opportunity to estimate seagrass emission factors. Methane emissions are generally assumed to be minor, but more research is still needed to confirm this assumption. There are few Australian estimates of emission factors. One recent example, Macreadie et al. (2015), found that seagrass in Jervis Bay NSW that had been destroyed over 50 years ago due to seismic testing had lost 72% of their original carbon stock, which dates back 100,000 years. They also found that recovered *Posidonia australis* meadows had only 35% of the carbon that an undisturbed meadow contained, yet more than twice that of disturbed areas. More of these estimates are needed across different habitats, climatic bioregions and for different causes of decline.

The term "**additionality**" refers to the requirement that the sequestration of carbon must be "in addition" to what would occur without offsets or policy action. That is, the sequestered carbon must be greater than the business-as-usual scenario for the country (Fig. 22.4).

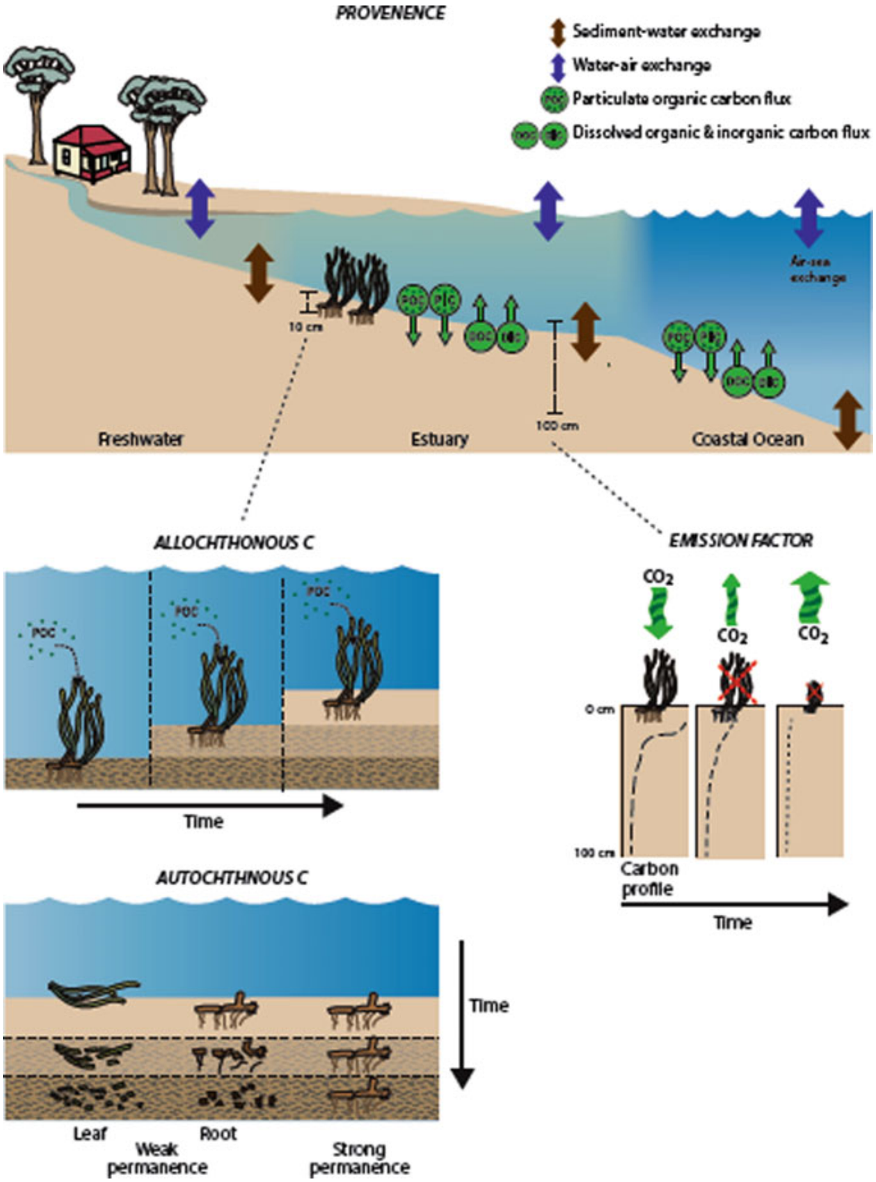

**Fig. 22.3** Provenance of seagrass carbon is shown across an estuary, where carbon enters from the terrestrial catchment and moves into the estuary where if it is not trapped then it can settle in the coastal ocean seafloor. Carbon can move from the water column into the sediment and it equilibrates with the atmosphere. Particulate organic carbon (POC) enters the sediment, while dissolved organic carbon and dissolved inorganic carbon is liberated from the sediment into the water column. The allochthonous carbon panel illustrates the process of sediment accretion and seagrass vertical migration. The autochthonous carbon panel illustrates the process of organic tissue breakdown of leaves and roots showing both weak and strong permanence. Finally, the panel showing emission factors demonstrates how the down-core carbon profile of a seagrass meadow contains more carbon than a recently degraded meadow, and significantly more that an aged degraded site

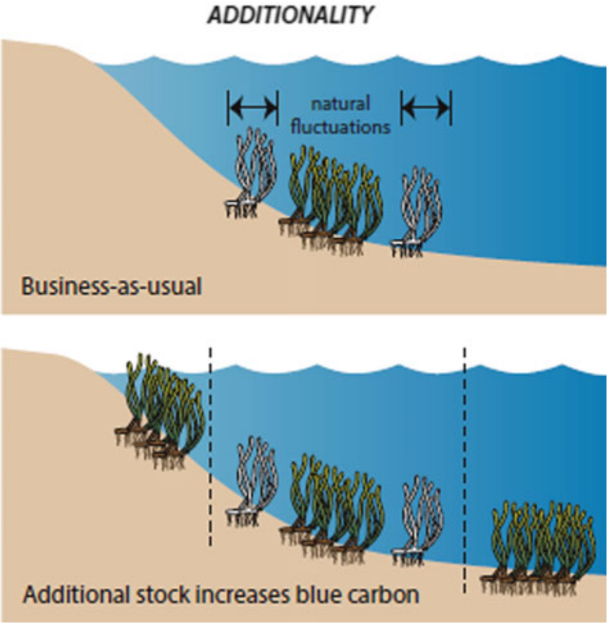

**Fig. 22.4** Additionality is illustrated in the lower panel where more seagrass biomass accumulated than the natural fluctuation (lighter coloured seagrass) in biomass that occurs over season and between years (upper panel)

"**Leakage**" occurs when activities within a project's accounting boundary affect regions outside of that boundary, and cause a change in the greenhouse gas (GHG) emissions of those external environments. Leakage is often unanticipated and difficult to quantify, particularly in hydrologically-connected coastal ecosystems. However, it is important that leakage is measured and included in the net GHG impact of a project. An increase in external GHG emissions is known as negative leakage, because it counteracts GHG benefits achieved within the project accounting boundary. Positive leakage occurs when external GHG emissions decrease as a result of a project activity. Positive leakage is an added benefit in a project's net GHG impact (Fig. 22.5).

The "**permanence**" of the carbon sequestered must be estimated and the risk of the loss must be minimised. Seagrass sediment carbon is well recognised as having high permanence due to the recalcitrance of the stored carbon (Trevathan-Tackett et al. 2015). However, some species are ephemeral, so the meadow will not always remain year-to-year. The degree to which the sediment carbon diminishes when the

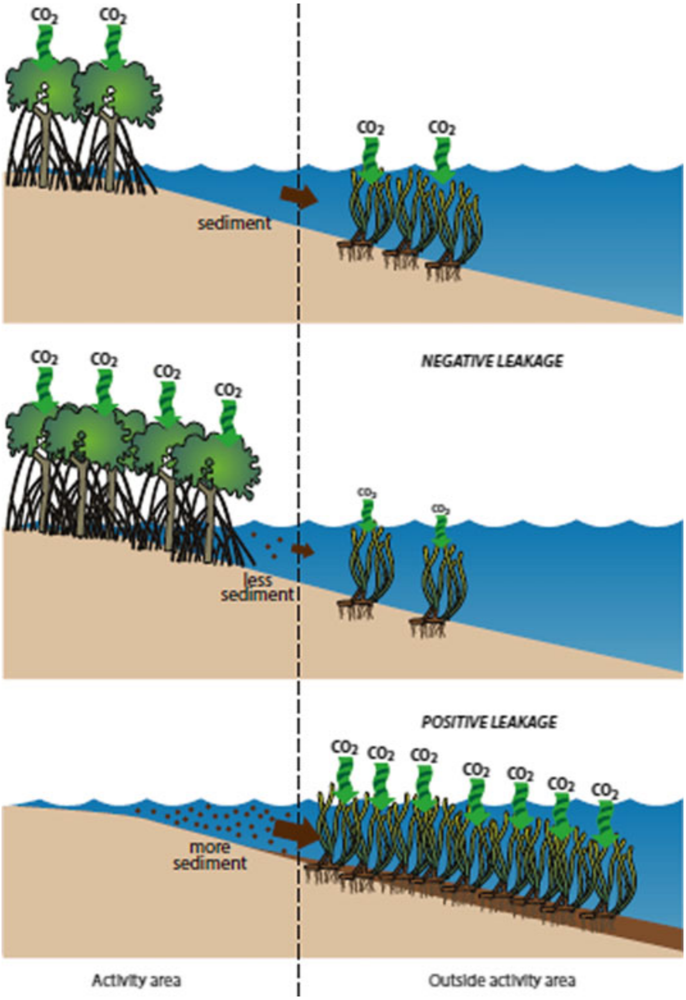

**Fig. 22.5** Leakage is illustrated in this panel, where leaves fall into the upper catchment, this created particulate organic carbon (brown dots) that is transported into the upper estuary (mangrove compartment), where mangrove leaves become part of the detritus within the mangrove carbon pool. Carbon that moves into the seagrass compartment has leaked from the mangroves. Pelagic phytoplankton move between the coastal ocean and the seagrass compartments

meadow disappears is currently unknown. Methods have recently been developed to assess the longevity of the carbon stored within the sediment cores. For example, thermogravemetric analysis can identify the lignocellulose matrix with seagrass sediments (Trevathan-Tackett et al. 2015). Furthermore, Macreadie et al. (2012) showed that shifts in the source of detritus altered the recalcitrance of sequestered carbon. The study also found that the source of allochthonous carbon in some seagrass meadows shifted during the past 200 years of human industrialisation from mangrove-dominated detritus to microalgae-dominated detritus.

Habitat "**conversion**" occurs when a blue carbon habitat is destroyed and replaced with an alternate function, such as removal of mangroves to establish shrimp ponds. The quantity of "carbon loss upon conversion" (Pendleton et al. 2012) must be estimated, but there are currently few Australian or global estimates. Conversion may only affect carbon stocks to a certain depth, but the depth at which conversion is no longer important is yet to be defined. Additionally, emission factors for converted habitats depend on how the habitat is converted. For example, dredging a seagrass meadow would likely release more of the carbon stock compared to less destructive conversions. Further research is needed to estimate the emission factors associated with different types of conversion.

Protecting seagrass also results in avoided emissions. In this case, a habitat's carbon stock is assessed, and if a land-management or a development proposal is considered for this region, the avoided emissions of the potential conversion can be assessed in the overall impact of the development. Avoided emissions vary depending on habitat carbon stock, the rate of carbon released to the atmosphere, the risk of future habitat loss and the cost of establishing a protection zone around the habitat. Preserving seagrass habitats can provide low-cost opportunities to mitigate $CO_2$ emissions.

## 22.8 Blue Carbon Accounting Processes in Australia

The National Carbon Accounting System (NCAS) currently accounts for Australian land-based GHG emissions (sources) and removals (sinks). The Australian Greenhouse Emissions Information System (AGEIS) was designed for Australia to meet IPCC requirements for national greenhouse inventory systems and reporting emissions. In addition to preparing the Australian National Inventory Report to meet the IPCC requirements, the Department of the Environment reports greenhouse gas (flux) information using the ANZSIC classification (ABS 2015). Accurate accounting requires knowledge of the biogeochemical cycles, satellite remote sensing and climatology, which are integrated using the Full Carbon Accounting Model (FullCAM; Ajani and Comisari 2014). Mangrove carbon stock estimates will be included for the first time in the next round of GHG reporting for Australia. However, questions still remain regarding boundaries between the different types of coastal, marine and terrestrial ecosystems, and boundary rules must still be developed. Similarly, thought must be given to how territory definitions encompass tidal movements and shifting seagrass meadows.

Carbon sinks must pass a ‘permanency’ test (e.g. 100 years in REDD) in order to qualify for carbon crediting systems (Grimsditch et al. 2013). It is unclear whether seagrass carbon reserves will be afforded special requirements for this test, as one might argue whether this is appropriate given the ephemeral and shifting nature of some seagrass species. Nevertheless, there is an urgent need to increase seagrass protection, restoration and monitoring efforts given their critical role in the global carbon cycle (Selig et al. 2014).

It is realistic to expect that seagrass will eventually be included in the national GHG accounting scheme, at which point all detected gains and losses of habitat will be incorporated into the national carbon budget. It is possible to create a blue carbon map of Australia’s coastal wetlands following the principles developed for Australia’s current terrestrial soil carbon map. Restoration (provided it is additional) would be counted as an increase in carbon storage and will be considered separately. Policies developed to encourage active carbon bio-sequestration such as the Carbon Farming Initiative are currently only relevant to mangroves and saltmarsh. Adopting coastal blue carbon measures for this recognition in the already well-established Carbon Farming Initiative may convince farmers to return ponded pastures to mangrove habitats. Given the many benefits of seagrass meadows, the advantages of linking of carbon storage with habitat conservation, biodiversity protection and valuation of ecosystem services is widely recognised (Barbier et al. 2011). Once included in the national carbon accounting, blue carbon will become an effective tool to enhance the conservation of seagrass.

## 22.9 Seagrass Blue Carbon Management

Economic policy and other incentives (e.g. stewardship-based incentives) that recognise the value of coastal blue carbon stocks and further sequestration are being developed in Australia and in many countries around the globe. It is hoped that a number of critical management actions, listed below, can be implemented to support and to promote blue carbon markets including the option for compensatory actions:

1. Identify the key regional threats to seagrass loss, e.g. dredging, boat mooring or coastal development. Monitor seagrass meadows on a regular basis to assess damage before effects cannot be reversed.
2. Identify vulnerable meadows with large carbon stocks as “high risk” and give such regions elevated protection status. This generally means areas of high carbon accumulation are allocated a high protection status as this would be a significant “avoided emission”.
3. Avoid destructive harvesting methods (e.g. purse seine netting) within seagrass meadows.

4. Support research to develop and test low cost, strategically-placed seagrass restoration that will promote natural recruitment and meadow development. Restoration of seagrass habitat could be an effective solution, but the process is complex. Generally 35–50% of restoration efforts are successful, and these have only covered small areas (Irving et al. 2010). In some cases, restored seagrass burial rates have been found to be similar to that of established meadows (Marba et al. 2015). However, Greiner et al (2013) found that meadows which had been restored 10 years ago as part of a seagrass restoration project in Chesapeake Bay, USA contained more carbon than bare sediments and 4-year old restorations; similar data are needed in the Australian context. Some cost-effective seagrass restoration methods have been developed, but seagrass restoration is still generally the most expensive among blue carbon habitats (Blandon and Ermgassen 2014; Hejnowicz et al. 2015). Therefore, it is much cheaper to maintain existing seagrass meadows and restore water quality to encourage natural recovery than directly fund the restoration of large seagrass meadows.

## 22.10 Conclusion

As policy supporting blue carbon is evolving rapidly, it is critical that science and observational data are used to inform these policy frameworks. For example, if and when a REDD-type policy is established for seagrasses, we will need to estimate C accumulation for a re-established meadow. Many nations are presently incorporating blue carbon into their broader GHG accounting schemes. Blue carbon accounting requires stocks and fluxes as well as estimates of processes including additionality, leakage, permanence, conversion and emission factors.

Development of seagrass carbon maps will assist with the impact assessment of coastal developments, where loss of carbon as well as seagrass community structure (and ecosystem services) will need to be mitigated. To extrapolate this new knowledge, biogeochemical models are currently being developed to predict blue carbon stock; where larger quantities of empirical data exist, the model estimates will be more accurate, whilst on-going improvements in remote sensing techniques will allow regular boundary updates of managed meadows.

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# Chapter 23
# Taxonomy of Australian Seagrasses

**John Kuo, Marion L. Cambridge, Len J. McKenzie**
**and Robert G. Coles**

**Abstract** This chapter lists all Australian seagrass species with their synonyms, which are currently accepted by the *IPNI* (International Plant Name Index) and the *Plant List*; the world authority of plant taxonomy. It also briefly reviews taxonomic studies on the Australian seagrasses and includes keys to all Australian seagrass species, with the practical goal of providing botanists with a name for seagrass species based on morphological characteristics. With their limited range of morphological characters, even constructing a morphological key presents some difficulties. The Australian waters are rich in seagrass species (33), with more than one third of the described seagrass species in the world. The majority of Australian temperate species are endemic, while those occurring in Australian tropics are also distributed in the Indo-Pacific region. Where possible we consider the results of molecular phylogenies but at present these are incomplete, and have only focused on a limited range of species.

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## 23.1 Introduction

Biological taxonomy is the science defining groups of biological organisms on the basis of shared characters and given names to these groups, a system originally developed by the Swedish scientist, Linnaeus (1753). Biological classification uses taxonomic ranks: Kingdom, Phylum, Class, Order, Family, Genus and Species. The named species should follow the '*International Code Nomenclature for algae, fungi, and plants (ICN)*, using the 'Binomial nomenclature' system to identify the genus to which the species belongs and the species within the genus.

It was Paul Ascherson, a German botanist working predominately on European and African terrestrial plants, who published the first studies on taxonomy and biogeography of seagrasses in 1868 and formally used the term 'Seegräser' in his publication titles from 1871. He defined the widely-held concept of 'seagrasses' as including the marine angiosperms, but excluded the genera *Ruppia* (now in the family Ruppiaceae) and *Lepilaena* (now in the Zannichelliaceae). Ascherson had probably not collected the seagrass material himself, but was sent the specimens by explorers, plant collectors and fellow botanists. He compiled and continued to update all taxonomic information available about seagrasses at the time, and listed all synonyms. Publications of Ascherson (1875, 1906), Ascherson and Gürke (1889) and Ascherson and Graebner (1907) provided a foundational classification of seagrasses in the world, which recognised eight genera, six tribes and two families. Ascherson described or redescribed about 20 seagrass species, which are still recognized. Unfortunately, most of type specimens of his named seagrass species were destroyed in the Berlin herbarium (B) during the WW II. Prior to Ascherson's seagrass works, there were about 20 currently recognized species described by earlier plant taxonomists, although some of generic names have been changed since, e.g., Linnaeus (1753) named *Zostera marina* and *Zostera oceanica* (now *Posidonia oceanica*) in Europe, Forsskål (1775) contributed *Zostera uninervis* (now *Halodule uninervis*) and *Zostera ciliata* (now *Thalassodendron ciliatum*) from the Red Sea.

## 23.2 A Brief History of Australian Seagrass Taxonomy

The early Australian seagrass taxonomy was based on works by early explorers and Ascherson's contributions. The British botanist Robert Brown visited Australia aboard the HMS *Investigator* (1801–1803) to collect and describe numerous new Australian plants including four seagrasses: *Amphibolis antarctica*, *Cymodocea serrulata*, *Halophila ovalis* and *Halophila spinulosa*, under the generic name *Caulinia* (Brown 1810). He also recorded the presence of what he assumed to be the Mediterranean species *Caulinia oceanica* (now *Posidonia oceanica*) from southern Australia. Subsequently, this species was described as a new species, *Posidonia australis,* by Hooker (1858) after he had visited Van Diemen's Land

(Tasmania) in 1840 as a naturalist with James Ross Clark's Antarctic expedition on the ship *Erebus.* It has been suspected that the material used by Labillardière (1807) to describe *Ruppia antarctica* (now *Amphibolis antarctica*) came from the Baudin (Nicolas Baudin) expedition (1800–1803) (see Ducker et al. 1977) to map the coast of New Holland (now Australia) with two ships*, Géographe* and *Naturaliste.*

Ferdinand von Mueller, appointed as the government botanist of Victoria in 1817 and arranged the purchase in 1883 of Otto W. Sonder's private herbarium which also contained seagrass material collected during Henry N. Moseley's global scientific expedition of the HMS *Challenger* (1872–76) from the Pacific and tropical eastern Australia (see Ducker et al. 1977). With these collections the National Herbarium of Victoria (MEL) had the most extensive collection of plant species specimens in Australia. A new seagrass collected by Mueller was described in 1867 by Irmisch as *Zostera muelleri* commemorating Mueller's contribution (Ascherson 1868). Mueller (1886) described a new seagrass as *Caulinia australiana,* a name that subsequently became a synonym of *Posidonia australis* based on specimens collected at King George Sound, Western Australia (see Cambridge and Kuo 1979). In his famous '*Phytographiae Australiae*", Mueller (1872–74) mentioned the following species of seagrasses: *Zostera muelleri*, *Z. tasmanica*, *Cymodocea serrulata*, *C. ciliata* (now *Thalassodendron ciliatum*), *C. antarctica* (now *Amphibolis antarctica*), *Posidonia australis*, *Halophila ovata* (now *H. ovalis*), *Caulinia spinulosa* (now *Halophila spinulosa*) and *Enhalus koenigii* (now *E. acoroides*). A similar seagrass species list appeared in the *Flora Australiensis* (Bentham 1878) but used *Zostera nana* for *Z. muelleri*, *Halophila ovalis*, *H. spinulosa* and added *Cymodocea isoetifolia* (now *Syringodium isoetifolium*). Local flora treatments, including seagrasses, were subsequently published from States and Territories, but only two species (*Posidonia australis* and *Cymodocea antarctica*) from Western Australia (Mueller 1902). Black (1915) described *Pectinella griffithii* (now *Amphibolis griffithii*) as a new species closely related to *A. antarctica*, based on the specimens collected from Henley Beach, South Australia. He also introduced the generic name *Pectinella* for these two species, as he felt that they were quite different from the rest of *Cymodocea*, but did not use this name in his flora treatment. Later he listed *P. australis*, *Z. nana*, *Z. tasmanica*, *C. antarctica*, *C. griffithii* and *H. ovalis* from South Australia (Black 1922–24).

The Danish botanist Ostenfeld (1914) reviewed the distribution of the world's seagrasses before visiting Australia in 1914. He found eight species of seagrasses on the coastline of Western Australia, including a new species, *Cymodocea angustata* and an unnamed *Posidonia* species from the Carnarvon area. Ostenfeld (1916) described and illustrated these, and considered that the differences between *A. antarctica* and *A. griffithii* were not of species rank. Later, Ostenfeld (1929) listed Australian seagrasses based not only on his own collections, but also on herbarium specimens in this country and overseas. The list consisted of 15 species in seven genera and two families, arranged according to Ascherson's taxonomic concept; *Amphibolis griffithii* and *Zostera tasmanica* were not included. The American botanist William Setchell had placed *Zostera tasmanica* in the new section (1933) and then transferred it into a subgenus in the genus *Zostera* (1935).

From that time, there were no major taxonomic studies of Australian seagrasses until the late 1960's. However, during this period several botanists suspected the existence of two species within *Posidonia australis*, which they attempted to differentiate on the basis of leaf width (e.g. Womersley 1956; Wood 1959; Eichler 1965). In the meantime, updated floras and species lists, including seagrasses, were published from several States. In a study of the genus *Halophila*, Doty and Stone (1966) described a new species, *H. australis*, based on herbarium material from Queenscliff, Victoria.

After his initial taxonomic contribution in the family Hydrocharitaceae for the *Flora of Malesia* in 1957 and visit to Australia in 1967, den Hartog published his seminal monograph "*The Sea-Grasses of the World*" in 1970, which provided descriptions for every known species and provided keys for their identification. He recognized 49 species, twelve genera, six subfamilies and two families. He defined the genera *Amphibolis*, *Cymodocea*, *Syringodium* and created a new genus *Thalassodendron* to replace a subgenus *Cymodocea* used by Ascherson and Graebner (1907) and Ostenfeld (1929); these four genera, together with the genus *Halodule* were placed within the subfamily Cymodoceoideae. Den Hartog also promoted the subgenus *Heterozostera* of Setchell (1935) to genus level, joining the genera *Zostera* and *Phyllospadix* in the subfamily Zosteroideae. Finally, the subfamily Posidonioideae was defined containing the genus *Posidonia*. Den Hartog (1970) included these three subfamilies of seagrasses, along with three subfamilies of freshwater aquatic plants, within the family Potamogetonaceae. In the family Hydrocharitaceae he placed three seagrass genera in three different subfamilies, Halophiloideae (*Halophila*), Thalassioideae (*Thalassia*) and Vallisnerioideae (*Enhalus*). He also omitted *Ruppia* in his seagrass monograph.

As far as Australian seagrasses are concerned, den Hartog recorded 23 species including three new species (*Zostera mucronata*, *Thalassodendron pachyrhizum*, and *Posidonia ostenfeldii*). He considered *Halophila australis* of Doty and Stone (1966) to be one of the four subspecies in *H. ovalis*. Den Hartog (1970) discounted the possibility that more than one species of *Posidonia australis* could be maintained solely on difference in leaf width, drawing attention to a clump of *P. australis* that he found cast ashore in Western Australia during a storm, which had both narrow and broad leaves apparently growing from a common rhizome. He attributed the difference in leaf width to a mixture of vigorous and senescent plants of the same species growing within the same meadow. In describing the new species *Posidonia ostenfeldii*, den Hartog selected as a holotype a specimen with very thin leaves collected from Esperance, Western Australia. The species which he recognized containing several leaf forms, including unnamed species *Posidonia* species recorded previously by Ostenfeld (1916). Aston (1973) in her '*Aquatic Plants of Australia*' followed closely the seagrass taxonomic treatment of den Hartog (1970).

Since that time increasing numbers of specimens have been collected from their natural habitats using SCUBA, grabs and benthic sledge, and as result several new taxa have been described. Ducker et al. (1977) contributed a taxonomic and biological description of the genus *Amphibolis*. Greenway (1979) described a new species, *Halophila tricostata*, from Lizard Island, the Great Barrier Reef; the species was placed in a new section, Tricostate of the genus *Halophila*. Cambridge and Kuo redefined the originally described Australian *Posidonia* species of *P. australis* (Cambridge and Kuo 1979) and *P. ostenfeldii* (Kuo and Cambridge 1984); it should be noted that *P. ostenfeldii* has an unusual terete leaf blade, round in cross section. They also described new species of *P. angustifolia* and *P. sinuosa* in the *P. australis* species group (Cambridge and Kuo 1979) and *P. denhartogii*, *P. robertsoniae*, *P. coriacea* and *P. kirkmanii* in the *P. ostenfeldii* species group (Kuo and Cambridge 1984). During the 1980's, McMillan and co-workers (McMillan 1982, 1983a, b, 1986, 1991; McMillan and William 1980; McMillan et al. 1981, 1983) used isozymes, secondary compounds and culture experiments to study Australian seagrasses including *Zostera*, *Amphibolis*, *Posidonia*, *Halodule* and *Halophila*, and also confirmed the species status of *Cymodocea angustata*. Jacobs and Williams (1980) clarified confusion over the citation of the type used in descriptions of the eastern Australian *Zostera*, by choosing lectotypes for each species; they also stressed that the separation of *Heterozostera* and *Zostera* at generic level was not convincing. This led Jacobs and Les (2009) to formally downgrade *Heterozostera* into the subgenus of genus *Zostera*. In her 'seagrasses' treatment, Robertson (1984) described two ecological forms of *Zostera muelleri*, restored *Halophila australis* to species status, and included three species of *Ruppia* via. *R. polycarpa*, *R. megacarpa*, *R. tuberosa* and a new named *Lepilaena marina* as "seagrasses". Larkum (1995) contributed a new seagrass species as *Halophila capricorni* from the Coral Sea. Kuo (2005) found that *Heterozostera* was not a monotypic genus but consisted of at least three Australian species, he redefined *H. tasmanica* and described two new species *H. nigricaulis* and *H. polychlamys*. Jacobs and Les (2009) transferred these *Heterozostera* species to the genus *Zostera*.

The formal taxonomic descriptions of family, genus and species of the Australian seagrasses (33 species, see Table 23.1 and also Kuo 2011), and certain *Ruppia* and *Lepilaena* species (5 species) as well as the species distribution maps can be found in the *Flora of Australia* vol. 39 (Wilson 2011). These species, with the exception of the genus *Heterozostera* and the species *Halodule tridentata*, are currently accepted by the *IPNI* (International Plant Name Index) and the *Plant List* of Royal Botanical Garden, Kew (RBG) and the Missouri Botanical Garden (MBG), the world authority in plant taxonomy.

**Table 23.1** Seagrass list in IPNI and Plant List compared with Australian Species

| | World | Australia |
|---|---|---|
| Family Zosteraceae | | |
| *Zostera*[a] | 13[a] | 3 |
| *Heterozostera*[b] | – | 3 |
| Family Posidoniaceae | | |
| *Posidonia* | 8 | 7 |
| Family Cymodoceaceae | | |
| *Cymodocea* | 4 | 3 |
| *Halodule* | 6 | 2 |
| *Syringodium* | 2 | 1 |
| *Amphibolis* | 2 | 2 |
| *Thalassodendron* | 3 | 2 |
| Family Hydrocharitaceae | | |
| *Enhalus* | 1 | 1 |
| *Thalassia* | 2 | 1 |
| *Halophila* | C. 20 | 7 |
| Family Ruppiaceae | | |
| *Ruppia* | C. 10 | 4 |
| Family Zannichelliaceae | | |
| *Lepilaenea* | 6 | 1 |

[a] Include *Heterozostera* species
[b] IPNI does not accept this genus

## 23.3 Species List—Australian Seagrasses and certain *Ruppia* and *Lepilaena* species

### Family Zosteraceae

**Genus *Zostera*** L. *Sp. Pl.* 2: 968 (1753) & *Gen. Pl.* ed. 5: 415 (1754)
**Subgenus *Zosterella*** (Asch.) Setch. *Amer. Naturalist* 69: 570 (1935)
***Zostera muelleri*** Irmisch ex Asch., *Sitzungsbar. Ges. Naturf. Freunde Berlin* 1867: 15 (1867)
Type: Australia felix, Nov 1852, *F. Mueller*, lecto: MEL, *file* SWL Jacobs & A Williams, *Telopea* 1: 454 (1980)
*Nanozostera muelleri* (Irmisch ex Asch.) Toml. & Posl. *Taxon 50: 433 (2001)*
*Zostera muelleri* sub. sp. *muelleri* SWL Jacobs, Telopea 11: 128 (2006)
*Zostera nana* var. *muelleri* (Irmisch ex Asch.) Kirk *Trans. & Proc. New Zealand Inst. 10: 392 (1878)*
***Zostera capricorni*** Asch., *Sitzungber. Ges. Naturf. Freunde Berlin* 1876: 11 (1876)
Type: Australia, Moreton Bay, Qld, 10 Oct. 1875, *[F.C.] Naumann*; lecto: UC, *fide*: SWL Jacobs & A Williams, *Telopa* 1: 454 (1980)
*Nanozostera capricorni* (Asch.) Toml. & Posl. *Taxon 50: 432 (2001)*
*Zostera muelleri* subsp. *capricorni* (Asch.) SWL Jacobs *Telopea 11:128 (2006)*

***Zostera mucronata*** Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2, 59: 91 (1970)

Type: Australia, Mandurah, W.A., in sandy estuary, 16 Aug. 1950, *GG Smith 274*; holo: L; iso: PERTH.

*Nanozostera mucronata* (Hartog) Toml. & Posl. *Taxon 50: 433 (2001)*

*Zostera muelleri* subsp. *mucronata* (Hartog) SWL Jacobs *Telopea 11:128 (2006)*

**Genus *Heterozostera*** (Setch.) Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 114 (1970)

***Heterozostera tasmanica*** (G. Martens ex Asch.) Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 116 (1970)

Type: Australia, Port Philips Bay, Vic., 1866, *F. Mueller*, lecto: MEL, *fide*: SWL Jacobs & A Williams, *Telopea* 1: 454 (1980)

*The Plant List*—as ***Zostera tasmanica*** M. Martens ex Asch. and listed *Heterozostera tasmanica* (G. Martens ex Asch.) Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 116 (1970) as synonym

***Heterozostera nigricaulis*** J. Kuo, *Aquatic Bot.* 81: 110 (2005)

Type: Australia, Kangaroo Is., site 91, S.A., 21 Nov. 1977, *H Kirkman (CSIRO 1988)*, holo: AD, iso: PERTH. *The Plant List*—stated as unsolved name

*Zostera nigricaulis* (J. Kuo) SWL Jacobs & Les *Telopea 12: 422 (2009*).

***Heterozostera polychlamys*** J. Kuo, *Aquatic Bot.* 81: 124 (2005)

Type: Australia, Flinders Bay, W.A., drift, 11 Dec. 1990, *H Kirkman (CSIRO 1751; CMM 260, 261*); holo: CANB, iso: MEL, PERTH.

*Zostera polychlamys* (J.Kuo) SWL Jacobs & Les *Telopea 12: 422 (2009).*

*The Plant List*—stated as unsolved name, but listed with the incorrectly spelled name *Heterozostera polychyamis*

## Family Posidoniaceae

**Genus *Posidonia*** KD Koenig, in *KDE Koenig & Sims*, *Ann. Bot.* 2: 95 (1805)

***Posidonia australis*** Hook. *f. Fl. Tasmania* 2: 43 (1858)

Type: Australia, George Town, Tasmania, in sea below low-water level, *R.C. Gunn 1347*; lecto: K, *file*: ML Cambridge & J Kuo, *Aquatic Bot.* 6: 317 (1979)

*Alga australis* (Hook.*f.*) Kuntze *Revis. Gen. Pl.* 2: 744 (1891)

*Caulinia australiana* F.Muell. *Fragm. 6: 198 (1868)*

*Caulinia oceanica* R.Br. *Prodr. Fl. Nov. Holl. 339 (1810*) [Illegitimate]

***Posidonia angustifolia*** Cambridge & Kuo, *Aquatic Bot.* 6: 312 (1979)

Type: Australia, 4 km NE of Cape Naturaliste, W.A., 30 m deep, 22 Nov. 1976, *ML Cambridge s.n.*, holo: PERTH, iso: K, ADU.

***Posidonia sinuosa*** Cambridge & Kuo, *Aquatic Bot.* 6: 309 (1979)

Type: Australia, Point Atwick, Garden Is., W.A., 3 m deep, 20 Nov 1971, *ML Cambridge*, holo: PERTH.

***Posidonia ostenfeldii*** Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 139 (1970)

Type: Australia, Esperance Bay, W.A., Dec 1951, *J Firman*; holo: AD.

***Posidonia denhartogii*** Kuo & Cambridge, *Aquatic Bot*. 20: 277 (1984)

Type: Australia, Albany, King George Sound, W.A., 8 m deep, 22 Dec 1981, *ML Cambridge & H Kirkman*, holo: PERTH, iso: AD, K, MEL, NSW.

***Posidonia robertsoniae*** Kuo & Cambridge, *Aquatic Bot*. 20: 281 (1984)

Type: Australia, King George Sound, W.A., 8 m deep, 22 Dec 1981, *ML Cambridge & H Kirkman*, holo: PERTH, iso: AD, K, MEL.

***Posidonia kirkmanii*** Kuo & Cambridge, *Aquatic Bot*. 20: 290 (1984)

Type: Australia, Israelite Bay, W.A., 10 m deep, 18 Dec 1981, *ML Cambridge & H Kirkman*, holo: PERTH, iso: AD, K, MEL.

***Posidonia coriacea*** Cambridge & Kuo, *Aquatic Bot*. 20: 285 (1984)

Type: Australia, Parmelia Bank, Cockburn Sound, W.A., 3.5 m deep, 6 Oct 1977, *ML Cambridge*, holo: PERTH.

## Family Cymodoceaceae

**Genus *Cymodocea*** K.D. Koenig, in *KD Koenig & Sims Ann. Bot.* 2: 96 (1805)

***Cymodocea rotundata*** Asch. & Schweinf. *Sitzungsber. Ges. Nauturf. Freunde* 1870: 84 (1870)

Type: not designated.

***Cymodocea serrulata*** (R. Br.) Asch. & Magnus, *Sitzungsber. Ges. Naturf. Freunde* 1870: 84 (1870)

Type: South coast of Australia, *R Brown Inter Austral 5813*; holo: BM.

*Caulinia serrulata* R.Br. *Prodr. Fl. Nov. Holl. 339 (1810)*

*Kernera serrulata* (R.Br.) Schult. & Schult.*f. Syst. Veg. 7(1): 170 (1829)*

*Posidonia serrulata* (R.Br.) Spreng *Syst. Veg. 1: 181 (1825)*

***Cymodocea angustata*** Ostendf. *Dansk. Bot. Ark*. 2(6): 10 (1916)

Type: Australia, Carnarvon, W.A., 31 Oct 1914, *CH Ostenfeld 271*, holo: C; iso: K, MEL.

**Genus *Halodule*** Endl. *Gen. Pl. sup*. 1: 1368 (1841)

***Halodule uninervis*** (Forssk.) Asch. in P.E. Bossier, *Fl. Orient*. 5: 24 (1882)

Type: not cited.

*The Plant list* as *Halodule uninervis* (Forssk.) Boiss.

Zostera uninervis Forssk. *Fl. Aegypt.-Arab. 157 (1775)*

*Halodule tridentata* (Steinh.) Endl. ex Unger. *Chlor. Protogaea* 67 (1843)

***Halodule pinifolia*** (Miki) Hartog, *Blumea* 12: 309 (1964)

Type: Japan, Okinawa Is., Yonagusuku Is., Uchina, Kagsuimura, Yakena, 22 July 1932, *S Miki*, KYO.

*Diplanthera pinifolia* Miki *Bot. Mag. (Tokyo) 46: 787 (1932)*

***Halodule tridentata*** (Steinh.) Endl. ex Unger. *Chlor. Protogaea* 67 (1843)

Type: Madagascar, *Du Petit Thouars*, P.

*Diplanthera tridentata* Steinh. Ann. Sci. Nat. II, 9: 98, Pl. 4 (1838)

**Genus *Syringodium*** Kütz. in: R.F. Hohenacker, *Algae Marine Exsicatae* 9: 426 (1860)

***Syringodium isoetifolium*** (Asch.) Dandy in *JE Dandy & G Tandy, J. Bot.* 77: 11 (1934)

Type: not cited.

*Cymodocea isoetifolia* Asch. *Sitzungsber. Ges. Naturf. Freunde Berlin 1867: 3 (1867)*

**Genus Amphibolis** C. Agardh. *Spec. Alg*. 1: 474 (1823)

***Amphibolis antarctica*** (Labill.) Sond. & Asch. ex Asch. *Linnaea* 35: 164 (1867)

Type: "Ad terrae Van-Leeuwin littoral", Esperance Bay, W.A., *Labillardiere*, holo: FI, iso: P.

The name was listed as unresolved by *The Plant List* and is accepted as *A. antarctica* (Labill.) Asch.

*Amphibolis bicornis* C.Agardh *Spec. Alg. 2(1): 474 (1823)*

*Amphibolis zosterifolia* C.Agardh *Spec. Alg. 2(1): 475 (1823)*

*Caulinia antarctica* (Labill.) R.Br. *Prodr. Fl. Nov. Holl. 339 (1810)*

*Cymodocea antarctica* (Labill.) Endl. *Gen. Pl. 230 (1837)*

*Cymodocea zosterifolia* (C.Agardh) F.Muell. *Syst. Census Austral. Pl. 1: 121 (1882)*

*Graumuellera antarctica* (Labill.) Reichb., Conspect. Reg. Veg. 43 (1828)

*Kernera antarctica* (Labill.) Schult. & Schult.f. *Syst. Veg. 7: 170 (1829)*

*Pectinella antarctica* (Labill.) J.M. Black. *Trans. & Proc. Roy. Soc. South Australia 37: 1 (1913)*

*Phucagrostis antarctica* (Labill.) Rupr. *Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 9(2): 60 (1852)*

*Posidonia antarctica* (Labill.) Spreng. *Syst. Veg. 1: 181 (1824)*

*Ruppia antarctica* Labill. *Nov. Holl. Pl. 2: 116 (1806)*

*Thalassia antarctica* (Labill.) F.Muell. Fragm. 4: 114 (1864)

***Amphibolis griffithii*** (JM Black) Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 208 (1970)

Type: Australia, Henley Beach, c. 10 km W of Adelaide, S.A., 1 Nov 1913, *HHD Griffith*, lecto: AD, *fide* E.L. Robertson in *HBS Womersley, Mar. Benthic Fl. South Australia* 1: 101 (1984); isolecto: MEL, NSW.

*Cymodocea griffithii* (J.M. Black) J.M. Black *Fl. S. Austral. 664 (1929)*

*Pectinella griffithii* J.M. Black *Trans. & Proc. Roy. Soc. South Australia 39: 94 (1915)*

**Genus *Thalassodendron*** Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 186 (1970)

***Thalassodendron ciliatum*** (Forssk.) Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 186 (1970)

Type: Yemen, Mocha, *P Forsskål*; holo: BM.

*Cymodocea ciliata* (Forssk.) Ehrenb. ex Asch. *Sitzungsber. Ges. Naturf. Freunde Berlin 1867: 3 (1867)*
*Zostera ciliata* Forssk. *Fl. Aegypt.-Arab. 157 (1775*)
***Thalassodendron pachyrhizum*** Hartog, *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Sect. 2 59: 194 (1970)
Type: Australia, Leighton Beach, W.A., drift, 30 July 1941, *AM Baird*, holo: PERTH.

**Family Hydrocharitaceae**

**Genus *Enhalus*** Rich. *Mem. Cl. Sci. Math. Inst. France* 1811 (2): 64, 74 (1814)
***Enhalus acoroides*** (L. f.) Royle. *Ill. Bot. Himal. Mts.* 1: 377 (1839)
Type: not located.
*Enhalus koenigii* Rich. *Mém. Cl. Sci. Math. Inst. Natl. France 12(2): 78 (1814)*
*Stratiotes acoroides* L.f. *Suppl. Pl. 268 (1782)*
**Genus Thalassia** Banks & Sol. ex KD Koenig in *KD Koenig & J Sims, Ann. Bot.* 2: 96 (1805)
***Thalassia hemprichii*** (Ehreb. ex Solms) Asch. *Petermanns Geogr. Mitt. 17: 242 (1871*)
Type: Eritrea, Massawa, 20–26, *Ehrenberg*, syn: BM, K, L, P. Lecto: BM, isolecto: K, P, L, *file*: Ferrer-Gallego and Boisset *Taxon* 64: 352 (2015)
*Schizotheca hemprichii* Ehrenb. ex Solms *Abh. Königl. Akad. Wiss. Berlin 1: 429 (1832)*

**Genus *Halophila*** Thouars, *Gen. Nov. Madagasc.* 2 (1806)
**Section Halophila** Asch., *Nuvo Giorn. Bot. Ital.* 3: 301 (1871)
***Halophila ovalis*** (R. Br.) Hook. *f.*, *Fl. Tasman.* 2: 45 (1858)
Type: Australia, Qld, *R. Brown Iter Austral 5816*, holo: BM; iso: RBGE.
*Caulinia ovalis* R. Br. *Prodr. Fl. Nov. Holl. 339 (1810)*
***Halophila minor*** (Zoll.) Hartog, *Fl. Males*. Ser. 1, 5: 410 (1957)
Type: Indonesia, Flores, near Bari, 12 July 1847, *Zollinger 3334*, syn: BM, L, P, NHMW.
*Lemnopsis minor* Zoll. *Syst. Verz. 75 (1854)*
***Halophila decipiens*** Ostend., *Bot. Tidsskr.* 24: 260 (1902)
Type: Thailand, off Koh Kahdat, Gulf of Thailand, Feb 1990, *J Schmidt 540*; holo: C; iso: L.
***Halophila capricorni*** Larkum, *Aquatic Bot.* 51: 320 (1995)
Type: Australia, Steve's Bommie, One Tree Is., Great Barrier Reef, Qld., 13 Nov. 1990, *AWD Larkum*, holo: NSW; iso: AD, SYD, UWA.
***Halophila australis*** Doty & BC Stone, *Brittonia* 18: 306 (1967)
Type: Australia, Queenscliff, Vic., Jan 1922, *Lucas*, holo & iso: NSW.
*Halophila ovalis* subsp. *australis* (Doty & B.C. Stone) Hartog *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2 59(1): 251 (1970)*

**Section Spinulosae** Ostenf., *Bot. Tidsskr*. 24: 240 (1902)

***Halophila spinulosa*** (R.Br.) Asch. in *G.B. von Neumayer. Anl. Wiss. Beobacht. Reisen* 368 (1875)

Type: Australia, *R Brown Inter Austral. 1815*, holo. BM *n.v.* (Apparently lost)

*Caulinia spinulosa* R.Br. *Prodr. Fl. Nov. Holl. 339 (1810)*

*Kernera spinulosa* (R.Br.) Schult. & Schult.f. *Syst. Veg. 7(1): 170 (1829)*

**Section Tricostata** M.Greenway, *Aquatic Bot*. 7: 67 (1979)

***Halophila tricostata*** Greenway *Aquatic Bot*. 7: 68 (1979)

Type: Australia, Lizard Is., Cook District, Qld, 1 Dec 1978, *M Greenway*, holo: BRI.

## Family Ruppiaceae

**Genus *Ruppia*** L. *Sp. Pl.* 127 (1735)

***Ruppia tuberosa*** J.S. Davis & Toml., *J. Arnold Arbor*. 55: 60 (1974)

Type: Australia, Salt ponds of Shark Bay Gypsum Pty. Ltd., on Heirisson Prong of Shark Bay, W.A., 5 Sept 1970, *JS Davis, s.n.*; neo: FLAS, *fide* SWL Jacobs & MA Brock, *Aquatic Bot*. 14: 321–322 (1982).

***Ruppia polycarpa*** R.Mason, *New Zealand J. Bot.* 5: 524 (1967)

Type: New Zealand, near mouth, Selwyn River, 27 Feb 1966, *J Clarke*, holo: CHR.

***Ruppia megacarpa*** R.Mason, *New Zealand J. Bot*. 5: 525 (1967)

Type: New Zealand, Taumatu, Lake Ellesmere, 9 Feb. 1966, *J Clarke*, holo: CHR.

***Ruppia maritime*** L. *Sp. Pl.* 1: 127 (1753)

Type: Plate 35 of P. Micheli, *Nov. Pl. Gen*. 72 (1729)

*The Plant List* had listed 50 synonyms!!

## Family Zannichelliaceae

**Genus *Lepilaena*** J. Drumm. ex Harv., *Hooker's J. Bot. Kew Gard. Misc*. 7: 57–58 (1855)

***Lepilaena marina*** E.L. Robertson, in *HB Womersley, Mar. Benth. Fl. South Australia* 1: 80 (1984)

Type: Australia, Port Clinton, Yorke Penin, S.A., 18 Nov 1981, *EL Robertson*, holo: ADU A 52656; iso: AD, MEL, NSW, PERTH.

## 23.4 Key to the Australian Seagrass and Certain Ruppia and Lepilaena Species

The following key is designed to identify all 'described' or known species in Australia from higher order of families, then to genera within the family, finally the taxon to specific genus.

By using vegetative and reproductive characters, and by following the sequential (key) key number each seagrass species can be identified. Each entrance has two options to follow until a particular family or genus or taxon is found. The primary key is modified and updated from Kuo and den Hartog (2001). The detailed identification key for each family, genus and species can be found in the *Flora of Australia* (2011).

1. Leaf strap-shaped with ligule present at junction of blade and sheath, pollen filiform, true marine **2**

1a. Leaf strap-shaped without ligule or petiolate without leaf sheath, pollen grains, true marine or estuarine **25**

2. Leaves without tannin cells; each longitudinal vein with several fibrous strands; one xylem lumen; flowers arranged on a spadix enclosed within a spathe **Zosteraceae 3**

2a. Leaves with tannin cells; each longitudinal vein without fibrous strands, and with several xylem lumens; flowers arranged in cymose inflorescences, or solitary, or paired on very short lateral branches **8**

3. Rhizome internode with 2 cortical vascular bundles; rhizome fibre bundles restricted to outer cortex; indeterminate wiry black erect stems absent ***Zostera* 4**

3a. Rhizome internode with 4–10 cortical vascular bundles; rhizome fibre bundles distributed in both outer and inner cortex or restricted to outer cortex; indeterminate wiry black erect stems present or absent ***Heterozostera* 6**

4. Blade with 3–5 longitudinal veins, apexes truncate. QLD, NSW ***Z. capricorni***

4a. Blade with 3 longitudinal veins, apexes variable in shape, but not truncate **5**

5. Blade apexes mucronate, with a distinct tridentate appearance. WA, SA ***Z. mucronata***

5a. Blade apexes notched to rounded, not mucronate. NSW, VIC, TAS ***Z. muelleri***

6. Wiry black erect stems present; blade apex obtuse with distinct central V-shaped notch; epidermal cells of blade with a distinct colliculate outer surface; erect stems occasionally bear up to 6 inconspicuous spathes forming indeterminate generative shoot. WA, SA, VIC, TAS, NSW ***H. nigricaulis***

6a. Wiry black erect stems absent; blade apex obtuse with minute slit or truncate with shallow notch; epidermal cells of blade with smooth outer surface; determinate lateral generative shoots present with 4–12 conspicuous spathes **7**

7. Rhizome fibrous bundles in both outer and inner cortexes; blade apex truncate with shallow notch, each spathe bearing 5–12 male and 5–12 female flowers. WA, SA. ***H. polychlamys***

7a. Rhizome fibrous bundles restricted to outer cortex; blade apex obtuse with narrow, minute slit, each spathe bearing 2–4 male and 2–4 female flowers. SA, Vic, Tas ***H. tasmanica***

8. Strap leaves develop from rhizome nodes without erect stem Posidoniaceae **9**

8a. Strap leaves develop on top of distinct erect stems Cymodoceaceae **16**

9. Leaf blade thin, not tough, concave-convex in cross section; fibrous strands restricted to epidermis and hypodermis, not in mesophyll *P. australis* species grouped **10**

9a. Leaf blade thick, tough, biconvex to terete; fibrous strands abundant extending into mesophyll *P. ostenfeldii* species group **12**

10. Leaf-sheath remaining intact, not disintegrating into a hairy fibrous mass; leaf-blade convex-concave, with epidermal cell in surface view with sinuose margins; blade fibre bundles more abundant in hypodermis than epidermis; fruit ellipsoid-terete. WA ***P. sinuosa***

10a. Leaf-sheath disintegrating into a hairy fibrous mass; leaf-blade flat, with epidermal cells in surface view with smooth margins **11**

11. Leaf blade 4–6 mm wide; longitudinal veins 7–11. Epidermal cells elongated, L/W ratio 0.5–6; blade fibre bundles associated with both epidermis and hypodermis; fruit pyriform. WA, SA, Tas ***P. angustifolia***

11a. Leaf-blade 6–20 mm wide; longitudinal veins 14–20; leaf-blade epidermal cells isodiametric in surface view, L/W ratio 0.5–1; blade fibre bundles associated more with epidermis than hypodermis. WA, SA, Vic, Tas, NSW ***P. australis***

12. Leaf-blade terete, rounded in cross section; longitudinal veins 3–5. WA ***P. ostenfeldii***

12a. Leaf blade biconvex, not rounded in cross section; longitudinal veins 5–17 **13**

13. Shoot with 1 or 2 leaves; sheath fibre bundles (apart from those adjacent to epidermis) occurring in a distinct layer separated from adaxial epidermis by two cell layers; leaf blade epidermal cell margins with fine corrugations. WA ***P. robertsoniae***

13a. Shoot with 2 to 3 leaves; sheath fibre bundles (apart from those adjacent to epidermis) evenly distribute among mesophyll, leaf blade epidermal cell margins smooth **14**

14. Leaf blade 1–2 mm wide; longitudinal veins 5–7; margins overlapping for almost the entire leaf sheath; sheath fibre bundles sparsely distributed amongst mesophyll. WA ***P. denhartogii***

14a. Leaf blade 2.5–6 mm wide; longitudinal veins 7–17, margins overlapping at most ¾ length of sheath, sheath fibre bundles abundant among the mesophyll **15**

15. Leaf blade 2.5–7 mm wide; longitudinal veins 7–9 (−11); leaf blade epidermal cells in cross section H/W ratio ca. 3–5. WA, SA ***P. coriacea***

15a. Leaf blade 6–10 (−12) mm wide; longitudinal veins 9–14 (−17); leaf blade epidermal in cross section H/W ratio ca. 1.5–25. WA ***P. kirkmanii***

16. Rhizome monopodial, herbaceous, with a short erect stem at each rhizome node. Leaf blade shed before leaf sheath. Produce fruits and seeds not viviparous **17**

16a. Rhizome sympodial, hard; elongated erect stem not at each rhizome node. Leaf blade and leaf sheath shed together. Viviparous reproduction **22**

17. Leaf blades subulate (round in cross section); flowers in cymose inflorescences. WA, Qld, NT ***Syringodium isoetifolium***

17a. Leaf blades flat, not rounded in cross section; flowers solitary **18**

18. Blade with 3 longitudinal veins, apex obtuse or with distinct lateral teeth; roots unbranched; anthers connate at different levels, style undivided ***Halodule*** **19**

18a. Blade with 7–17 longitudinal veins, apex truncate or obtuse with regularly or sparse spaced teeth; roots branched; anthers connate at same level, style divided into two stigmata ***Cymodocea*** **20**

19. Bade apexes obtuse, with minute serrations, lateral teeth little developed or absent. WA, Qld, NT ***H. pinifolia***

19a. Blade apexes with a distinct tridentate appearance, lateral teeth well-developed. WA, Qld, NT ***H. uninervis***

20. Leaf scars closed; old sheaths form a scarious mass; blade apex rounded to obtuse, faintly serrulate; rhizome internodes without cortical fibrous strands WA, NT, Qld ***C. rotundata***

20a. Leaf scars open; old sheath not forming scarious mass; rhizome internodes with cortical fibrous strands **21**

21. Blade 4–9 mm wide, 13–17 longitudinal veins, blade apex rounded to obtuse, distinctly serrulate; leaf sheath broadly triangular, narrowed at base; rhizome internode cortical vascular bundles free from fibrous strands. WA, NT, Qld ***C. serrulata***

21a. Blades 3–6 mm wide, 9–13 longitudinal veins, apex obtuse to slightly attenuate, sparsely serrate, sometimes bifurcate; leaf sheath slightly obconic; rhizome internode cortical vascular bundles associated with fibrous strands. WA ***C. angustata***

22. Erect stems much branched at irregular rhizome node intervals; roots much branched at each rhizome node; leaf blade apex bidentate; anthers with 2 or 3 branched appendages, stigmata 3; viviparous seedling with combs like grappling apparatus ***Amphibolis* 23**

22a. Erect stems, little or not branched at every fourth rhizome node; roots at node preceding stem bearing rhizome node; blade apex rounded, coarsely denticulate; anther with 1 appendage, stigmata 2; viviparous seedling with an enlarged innermost floral bract, without comb-like grappling apparatus ***Thalassodendron* 24**

23. Leaf sheath overlapping with their lower half only; blade usually twisted about 180° in the distal half, apex truncate or semi-circularly notched, with 2 acute lateral teeth. WA, SA, Vic, Tas ***A. antarctica***

23a. Leaf sheath overlapping along their full length; blade little (less than 90°) or not twisted in upper part, apex notched with 2 obtuse lateral teeth. WA, SA ***A. griffithii***

24. Roots 2 at rhizome node, 3–5 mm thick, little branched, with black surface. WA ***T. pachyrhizum***

24a. Roots 1–5 at rhizome node, 0.5–2 mm thick, much branched, wiry, with light brown surface. WA, NT, Qld ***T. ciliatum***

25. Leaves broad, either strap-shaped without a ligule or a distinct broad petiolate without a leaf sheath, auricles absent, marine habitats Hydrocharitaceae **26**

25a. Leaves thin, less than 1 mm, with 1–3 longitudinal veins, leaf sheath presence, brackish water, seldom marine **34**

26. Leaves strap-shaped with many longitudinal vascular bundles, leaf sheath present **27**

26a. Leaves with a distinct petiolate, blades oblong or lanceolate to ovate, not strapped shape, leaf sheath absent ***Halophila* 28**

27. Rhizome monomorphic, covered with long black bristles; roots cord-like, root hairs sparse and inconspicuous. WA, NT, Qld ***Enhalus acoroides***

27a. Rhizome dimorphic, a scale at node; short erect foliage-bearing shoots at irregular intervals of rhizome nodes; brownish fibers at the base of the shoots, root hairs abundant, conspicuous. WA, NT, Qld ***T. hemprichii***

28. Erect lateral shoot elongate bearing leaves in pseudo-whorl or in many pairs of sessile leaves; flowers on apical nodes of erect lateral shoot **29**

28a. Erect lateral shoots extremely short bearing 1 pair of petiolate leaves; flowers mostly on rhizome nodes **Sect. Halophila 30**

29. Leaves in 10–20 pairs distichously arranged on each lateral shoot; rhizome and lateral shoot wiry **Sect. Spinulosae** WA, NT, Qld ***H. spinulosa***

29a. Leaves in 2 or 3 pseudo-whorls at each node of lateral shoot; rhizome and lateral shoot fleshy **Sect. Tricostatae**. Qld ***H. tricostata***

30. Monoecious; blade hairy, but occasionally glabrous, the margin finely serrulate; petiole shorter than blade **31**

30a. Dioecious; blade glabrous, the margin entire; petiole mostly as long as or longer than blade **32**

31. Male and female flowers on separate spathes of the same plant; blade surface usually with few stiff hairs. Qld ***H. capricorni***

31a. Male and female flowers on the same spathe; blade surface usually with fine hairs WA, NT, Qld, Vic ***H. decipiens***

32. Female flowers and fruits on extended floral shoots; styles 6; leaf blade linear-lanceolate to elliptical, c. 3–6 times as long as wide, membranous. WA, SA, Vic, Tas ***H. australis***

32a. Female flowers and fruits on rhizome node; styles 3; leaf blade ovate, oblong, or elliptic, c. 1.5–2 (–4) times as long as wide, not membranous **33**

33. Leaf blade 5–12 mm long, cross veins 3–10 on each side of midrib. WA, NT, Qld ***H. minor***

33a. Leaf blade 10–45 mm long, cross veins 12–24 on each side of midrib. WA, NT, Qld, NSW ***H. ovalis***

34. Leaf blade with a single median vein, ligule present, perianth present, fruit an achene. WA, SA, Vic, Tas ***Lepilaena marina***

34a. Leaf blade with 3 longitudinal veins, ligule absent, perianth absent, fruit is drupaceous. ***Ruppia* 35**

35. Mature fruiting carpels sessile or subsessile, the podogyne always much shorter than the carpel. WA, SA, Vic ***R. tuberosa***

35a. Mature fruiting carpels with an elongate podogyne always longer than the carpel **36**

36. Pollination occurring below water surface; peduncle usually less than 5 cm with none or once to twice loosely coiled. Cosmopolitan **R. maritima**

36a. Pollination occurring above water surface; after the pollination, the developing inflorescence retracted below water surface by a up to 10 cm long coiling peduncle **37**

37. Blade apexes obtuse; carpels mostly (4–) 6–8 (–16); endocarp perforations narrowly triangular WA, SA, Qld **R. polycarpa**

37a. Blade apexes bidentate or truncate; carpels (2–) 4 (–6); endocarp perforations broadly triangular. WA, SA, Vic **R. megacarpa**

## 23.5 Discussion and Concluding Remarks

This chapter has the practical goal of providing botanists with a name for seagrass species based on morphological characteristics. With their limited range of morphological characters, even constructing a morphological key presents some difficulties. Where possible we consider the results of molecular phylogenies but at present these are incomplete, and have only focused on a limited range of species. Alves and Filho (2007) stated that 'Any one dealing with inventories of plant diversity constantly uses morphological determination keys. Molecular systematics still cannot replace traditional determination techniques, and a simple morphological system is still a practical and cheap way to find out a taxon's true identity'.

The higher order taxonomic classification of aquatic angiosperms including seagrasses has been very confused in the past. The taxonomic treatment of seagrasses has been subject to various schemes since Ascherson's works (1867 to 1907), as discussed by den Hartog (1970) and den Hartog and Kuo (2006). With the recent contribution of molecular phylogentic studies by the *Angiosperm Phylogeny Group System* (APG 1998 and APG II 2003) (see also Petersen et al. 2015), all aquatic plants have been placed in the order Alismatales containing 13 families. Seagrasses have been classified in three marine families of Zosteraceae, Posidoniace and Cymodoceace, together with three genera, *vis*. *Enhalus*, *Thalassia* and *Halophila* in the family Hydrochartiaceae. For the genera, *Ruppia* and *Lepilaena* belonging to the family Ruppiaceae and Zannichelliaceae respectively, not all species are associated with marine environments, so while we have included them there remains debate whether they should be considered as 'seagrasses'.

Prior to 1970, the family Zosteraceae consisted of two genera: *Phyllospadix* and *Zostera* with three subgenera (*Zostera* s.s., *Zosterella*, *Heterozostera*). There has been an on-going discussion about generic boundaries within the family Zosteraceae since den Hartog (1970) elevated the subgenus *Heterozostera* Setch. to genus status (see Jacobs and Williams 1980; Les et al. 1997; Tomlinson and Posluszny 2001; Tanaka et al. 2003; Kato et al. 2003). Tomlinson and Posluszny (2001) upgraded the subgenus *Zosterella* to genus status under the name of

*Nanozostera*, resulting in the Zosteraceae then containing four genera, i.e. *Zostera, Heterozostera*, *Nanozostera* and *Phyllospadix*, with no subgenera in the genus *Zostera*. Under this scheme, all Australian *Zostera* (*Zosterella*) species were then included in *Nanozostera* as *N. muelleri*, *N. capricorni*, and *N. mucronata* respectively (see Tomlinson and Posluszny 2001). On the other hand, Jacobs and Les (2009) formally downgraded *Heterozostera* to one of three subgenera of the genus *Zostera*, so that the family Zosteraceae consisted of only two genera *Phyllospadix* and *Zostera* with three subgenera as the prior 1970s taxonomic arrangement. Kuo (2005) showed that the *Heterozostera* is not a monotypic genus but consisted of at least three species in Australia based on morphology and biology. He recommended that further detailed classical and molecular comparative studies on all species in *Zostera* and *Heterozostera* should be conducted to determine the generic boundary of *Zostera*, *Heterozostera* and *Nanozostera*. Without such new information, den Hartog and Kuo (2006) and Kuo (2011) retained *Heterozostera* as a genus and *Zosterella* as a subgenus of *Zostera*, despite the *IPNI* (at April 2012) listing of only two genera in the family. More recently, Coyer et al. (2013)'s molecular study using gene markers (*ITS1, matK, rbcL, psbA-trnH*) demonstrated four genera in the family Zosteraceae as proposed by Tomlinson and Posluszny (2001) and contrary to Les et al. (1997)s concept of only two genera in the family; *Phyllospadix* and *Zostera*, with three subgenera (*Zostera* s.s., *Zosterella* and *Heterozostera*) in the genus *Zostera*. However, in view of the contrasting findings of molecular phylogenic studies by Les et al. (1997, 2002) and Coyer et al. (2013), we have therefore maintained the three genera in the family of Zosteraceae (Hartog 1970; Hartog and Kuo 2006; Kuo 2010) in this chapter.

Les et al. (2002) considered the three Australian *Zostera* described species under a single species as *Z. capricorni* initially and then as *Z. muelleri* later due to the priority issue (Jacobs et al. 2006), and they treated *Z. mucronata* and *Z. capricorni* as subspecies of *Z. muelleri*. On the other hand, Coyer et al. (2013) had distinguished *Z. mucronata* from *Z. muelleri* and *Z. capricorni*, but they could not separate the two latter taxa on a molecular basis. It should be stressed that *The Plant List* accepts three distinct Australian *Zostera* species; *Z. muelleri*, *Z. capricorni* and *Z. mucronata* and without subspecies.

Soon after the revision of the genus *Heterozostera* with the three new species by Kuo (2005), Jacobs and Les (2009) had transferred all these *Heterozostera* species under the genus *Zostera*. Subsequently, The *IPNI* (at March/April 2012) accepted the name of *Zostera tasmanica* and treaded the newly named *Heterozostera nigricaulis* and *H. polychlamys* as unresolved names but stated as likely under the genus *Zostera* as proposed (Jacobs and Les 2009). These taxonomic arrangements by the *IPNI* most likely occurred prior to the Coyer et al. (2013) molecular study. For this main reason, we maintain and accept all named species under the genus *Heterozostera*. Lack of the separation with molecular markers has also arisen in Coyer et al. (2013) who could not distinguish *H. tasmanica* from *H. nigricaulis*, despite the very obvious morphological and distributional differences in these two species. This may have been the result of only one specimen of *H. tasmanica* being analyzed; this species appears to be far more difficult to locate *in situ* than would be expected from its earlier status before the revision of the genus by Kuo (2005).

Campey et al. (2000) re-evaluated the species boundaries in the members of the *Posidonia ostenfeldii* species complex from one locality and concluded that *P. coriacea* and *P. robertsoniae* are not different species. Recently, Aires et al. (2011) using a nuclear marker (*rRNA-ITS*) could only recognize Australian *Posidonia australis*, *P. angustifolia*, *P. sinuosa* and the *P. ostenfeldii* species group, but could not resolve four taxa within the *P. ostenfeldii* species complex. They considered that the four formally described taxa were different morphotypes or ecotypes of the same species. These four taxa co-exist certain areas in SW Australia, particularly on the southern coast of Western Australia but are not well-studied or collected over their geographic ranges. *Posidonia coriacea* extends furthest north and has the widest distribution within the *P. ostenfeldii* species group from Coral Bay in the Ningaloo coral reef to South Australia.

*The Plant List* currently accepts six species in the genus *Halodule* containing two Old World species, *Halodule uninervis and H. pinifolia*. On the other hand, Waycott and Barid (see Waycott et al. 2006) could only recognize three species in the genus *Halodule*, i.e. *H. uninervis*, *H. pinifolia* and *H. wrightii* using ITS markers. It has been long recognized that *Halodule uninervis* having two leaf forms (wide and narrow) (den Hartog 1970; Kuo and den Hartog 2001). McMillian (1983b) found that both wide and narrow leaf forms of *H. uninervis* from Shark Bay, W.A., maintained their original morphology in long-term culture. Furthermore, Sidik and Harah (1999) demonstrated that these two forms could be distinguished by vegetative and reproductive morphology, together with habitat preferences. Ohba and Miyata (2007) redescribed the two species as *H. uninervis* and *H. tridentata* from Japan, and these authors even found a hybrid between these two taxa in Okinawa Is. Den Hartog and Kuo (2006) considered that the narrow-leave forms of *H. uninervis* should be named as *H. tridentata*. Kuo (2011) formally included *H. tridentata* in the *Flora of Australia* as a species occurring across northern Australia. Ito and Tanaka (2011) reported a hybrid between the wide and narrow leaf forms of *H. uninervis* using plastid and nuclear DNA evidence, though these authors did not use the name of *H. tridentata* for the narrow leaf form. However, *The Plant List* (at March 2012) treated *H. tridentata* as a synonym of *H. uninervis*, thus we do not include *H. tridentata* as a distinct species here. The taxonomy of the genus *Halodule* remains contentious and it is almost certain there will be future changes.

Among five sections in the genus *Halophila*, Section Americanae with two species is occurring only in the American continents. Sections of Spinulosae and Tricostatae consist of a single species each, *H. spinulosa* and *H. tricostata*, respectively, both originally described from Queensland. The Section Microhalophilae, also consists of a sole species, *H. beccarii*, described from northern Borneo, Malaysia, and is widely distributed in the Gulfs of Thailand and Bengal, even extending to Taiwan (at 24°N) (Kuo et al. 2006).

The fifth Section Halophila represents the morphologically most diverse group, either monoecious or dioecious, and composed of rather delicate plants that make the taxonomy of this group extremely difficult. Currently, only five of the 13 *IPNI* accepted species are listed in Australia, i.e. *Halophila ovalis*, *H. minor*, *H. capricorni*, *H. decipiens* and *H. australis* (Kuo 2011), and the type locality of *H. ovalis* and *H. capricorni* was in Queensland. Early molecular studies using ITS markers could not distinguish various morphologically distinct species, including *H. australis* (Waycott et al. 2002). Subsequent molecular studies confirmed the existence of *H. australis* and *H. major* from SE Australia (Uchimura et al. 2008) and from SW Australia (Kuo per. comm. 2007). On the basis of the type specimen (*H. Zollinger 3430*), *Halophila major* (*The Plant List* accepted the taxon) appears to occur in northern but not in southern Australia (Kuo, unpubl.). In view of these inconsistencies, *H. major* has not been included in the *Flora of Australia* (Kuo 2011) or in this Chapter. Indeed, there are several morphologically rather distinct *Halophila* populations with different habitats and distributions in Australia (Kuo, pers. obs.) that require more careful studies in the near future.

Current molecular genetics approaches still cannot resolve taxonomic issues in seagrasses. ITS sequences have proved to be useful in determining genetic level boundaries, except that of *Heterozostera* but do not have resolution for identifying species in the genera *Zostera, Posidonia*, *Heterozostera*, *Halophila* and *Halodule*. A whole genome sequencing approach (Shendure and Ji 2008) or techniques developed in the near future may improve our understanding of the species boundaries in these genera. Until that time, we should not discount the currently described Australian seagrass species recognized by the *IPNI*.

It may take some experience to recognize species as they are currently defined but in the case of *Posidonia* species, we consider that merging them could end up losing important information. In some cases molecular analyses do not find clear differences but at this stage, we have retained them.

We highly recommend that all future molecular studies conduct analyses using multiple samples from across the species range, and particularly including the species type locality. In addition, voucher specimens of the study material should be deposited into recognized herbaria to provide material for traditional taxonomic studies of correct ‘species identification’. The study material of any scientific research in fields such as ecology, physiology, biochemistry, etc. requires a ‘species name’ that is based on traditional taxonomic species identification and at this stage of development of molecular techniques this cannot be replaced by identification based on molecular approaches.

Finally, we would like to draw attention to the fact that for seagrasses to adapt and complete their life cycle in marine environment, they have evolved much simpler plant structures than many other plant groups (see more detail in the following chapter). Thus, the morphological and anatomical characters that can be used for taxonomical purpose in seagrasses are rather limited in comparison to those in many terrestrial monocotyledonous plants. Identifying seagrass species is not always easy, particularly for sympatric species or for very small species such as *Halophila* that may require a microscope for adequate identification. In the meantime, we encourage more field studies, particularly details of reproductive morphology and biology and the lodging of voucher specimens in recognized herbaria for the future improvement in seagrass taxonomy.

## Appendix

The editors take the opportunity to include as an Appendix a "Taxonomy of Australian Seagrasses", which sets out a taxonomy based on classical taxonomic criteria. Molecular techniques have provided a new way of classifying organisms and this has happened to some extent with seagrasses. Chapter 5 presents much of this recent evidence and discusses the issues. Of particular relevance here is the issue over the previous seagrass genus *Heterozostera (Zosteraceae)*. According to some experts, *Heterozostera* cannot be supported any more and should be merged into the genus *Zostera* (see Les et al. 2002; Jacobs and Les 2009). Les et al. (2002) looked only at *Heterozoster tasmanica*, and concluded that it should be transferred to *Zostera* as a sub-genus, *Heterozostera*. However, Jacobs and Les (2009) assumed that *Heterozostera tasmanica* was so difficult to separate from the other two *Heterozostera* species, that they chose not to recognise it as a separate species, leaving only *Z. nigricaulis* and *Z. polychlamys* as legitimate Australian species. If this were followed there would be 3 new *Zostera* species, Z. *chilensis* (from Chile), *Z. nigricaulis* (formerly *Heterozostera nigricaulis and H. tasmanica;* from Australia) *and Z. polychlamys,* (formerly *Heterozostera polychlamy;* from Australia) all of which would be placed in the sub-genus *Heterozostera.* This new approach has not been adopted by all Australian authorities but the International Plant Name Index prefers not to recognise the genus *Heterozostera*. Some workers, including the authors of the Appendix still advocate *Heterozostera tasmanica*.

Notwithstanding this difference in opinions the Appendix presents much useful taxonomic and systematic information together with keys of the Australian seagrass and pseudo-seagrass species, which will be very useful to Australian seagrass workers.

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# Conclusions

From the wide coverage of nearly all aspects of biology it is easy to scan across the chapters in this book and see that blessings of biogeography (the collision of a Gondwana flora with a the tropical triangle of diversity for corals, mangroves and seagrasses) combined with one of the most research-oriented communities in the world has yielded a fascinating scientific page turner not only for seagrasses but for many biological disciplines as well.

How, seagrasses evolved (Chap. 1) is not just a story for Australia; but today Australia features large in the story. It is one of humble beginnings of early seagrasses alongside freshwater plants leading to special adaptations (Chaps. 11 and 12), that allowed the seagrasses to colonise most of the shorelines of the world. Almost undoubtedly the initial success of seagrasses led to the evolution of sirenian herbivores (Chap. 1), which in turn led to a great reduction in species and biomass, for both sirenians and seagrasses. Today the success of dugongs in Australian waters is an outcome of the abundance of seagrasses in northern Australia, and the limited harvesting of this population by local indigenous communities (Chap. 16).

How the seagrasses evolved and what forms they took is outlined in Chaps. 1, 4 and 5. And where and how these seagrasses formed communities is discussed in Chaps. 2, 3, 9, 10 and 14. Chapter 4 gives a detailed account of the structure and anatomy of Australian seagrasses, which because of the high diversity of seagrasses in Australia affords a fairly comprehensive look at seagrasses altogether. And leading on from this, the Taxonomy of Australian Seagrasses is given finally; that is how to identify seagrasses in the field, which is a very valuable contribution to what otherwise might have been a very academic exercise in structure and function.

The influence of molecular biology has been a profound area of research in seagrasses as with other disciplines. Chapter 5 discusses how this has influenced new approaches to seagrass systematics by phylogenetic analyses. And Chap. 6 discusses how genetic approaches can open up our understanding of how the special reproductive systems and local distributions can influence distributions on a continental scale. However, whole genome approaches which have only a few mentions in chapters of this book (see Olsen et al. 2016; Lee et al. 2016) will

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undoubtedly lead to new ways of looking at these and many aspects of seagrass biology.

Seagrass resilience, like that observed in corals, is a complex of interactions between seagrasses, competitors and consumers, and the environment across a range of space and time scales. Resilience (Chap. 7) and resistance (Chap. 10) in seagrasses are explored with Australian examples. Similarly the processes and vectors of recovery are investigated through assessing our understanding of reproduction dispersal and recruitment in seagrasses (Chap. 8) connectivity among seagrass meadows (Chap. 6) and the dynamics of seagrass seascapes over decades and across square kilometres (Chap. 9).

The new revolution in robotics and machine learning will drive our remote data gathering in seagrass ecosystems, and combined with remote sensing will define our monitoring of seagrass condition and health into the future. Advances in analysing remotely sensed data (Chaps. 9 and 15) has developed to the point where we can see changes over time in seagrass distributions at the level of the seascape. Being able to determine temporal change at seascape scales has influenced theory and modelling of resilience (Chap. 7) and resistance (Chap. 10) in seagrasses. These advances have also allowed us to assess seagrass loss and the scale of restoration and intervention needed to maintain a resilient seagrass ecosystem (Chap. 20) which also influences Blue Carbon accounting (Chap. 22).

The importance of seagrass ecosystems in tropho-dynamics and plant-animal interactions (Chaps. 16, 17, 18 and 19) continues to be a popular area of research. Our understanding of the role of seagrasses in ecosystem resilience and the complexity of trophic interactions in seagrass meadows has increased dramatically from these recent studies (Chap. 7). Behavioural studies have also expanded our understanding to include the effect of predators and “fear responses” in herbivores on grazing (Chap. 16).

Modern threats to seagrasses including global warming and acidification (Chap. 21), add to existing pressures driven by human activity on the coastal zone (Chap. 20) associated with: light deprivation (Chap. 10) and its effect on photosynthesis and metabolism of seagrasses (Chap. 11); water quality and sediment stressors (Chap. 14) and their influence on the microbiology of seagrass habitats (Chap. 12) and seagrass sediment interactions (Chap. 13). The re-evaluation of root rhizospheres and microbial communities (metagenomics) and their interactions with sediment chemistry combined with fine scale localisation tools like fluorescent in situ hybridization (FISH) and nano secondary ion mass spectroscopy (nanoSIMS) are revolutionising our study of plant-microbe interactions and our understanding of the importance of sediment condition in seagrass health.

The future for seagrass research in Australia and globally is under increased pressure to address threats to seagrasses across local to global scales, to inform management rapidly, to preserve extant seagrasses and to restore lost ecosystems. This book lays out the foundations for the next decades, and will inform future generations of the current status for seagrass research in Australia at the present time. Going back to Chap. 1, we still have a very inadequate knowledge of how the 3 (or more) families of flowering plants gave rise to the seagrasses and why out of these families, which produced many thousands of species altogether, there are only 60 plus species of seagrasses extant in the world today. If we could explain these evolutionary events we would be in a much better position to predict changes into the future. Clearly, even as we write, perceptions are changing, and new questions and new techniques are developing rapidly. The recent research into the genome of seagrasses offers a deeper understanding of the evolution of seagrasses as they adapted back into a fully submerged life. The genome also offers the potential for rapid assessments of environmental impacts through greater understanding of the genome-transcriptome-metabolome-plant nexus. For example, whole genome analysis has also allowed for a greater understanding of the importance of microbes in seagrass rhizospheres. Another area of growth has been the focus on scaling and resilience under a globally changing climate and the impact of increased human developments along our coasts. This has led to the emergence of new tools and practices to remotely sense impacts and to predict loss of resilience of seagrasses into the future. We are at a crossroads, but without fundamental understanding of the structure and function of the plant we cannot accurately determine cause and effect pathways and understand seagrass loss. This book captures both the existing and the potential knowledge of seagrasses of Australia in one volume and we hope that it will become the reference for seagrass research both nationally and internationally.

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