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Chapter 7
Seagrass Dynamics and Resilience

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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 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;

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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

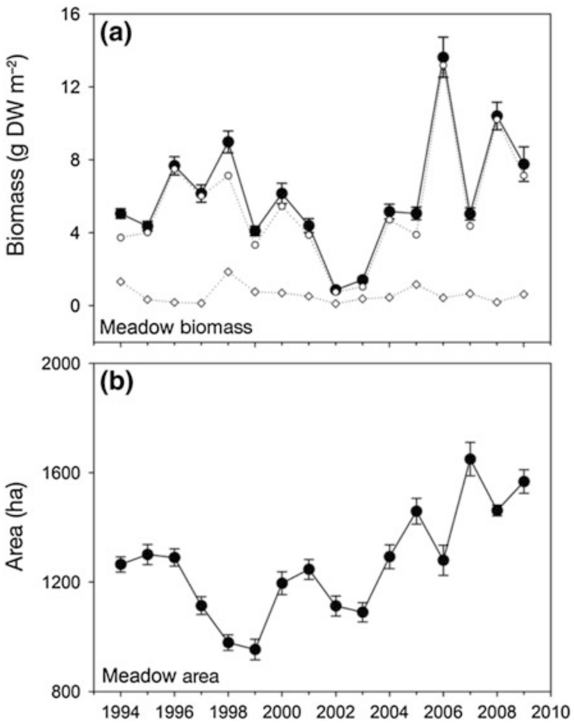

Fig. 7.1 Dynamic change in seagrass biomass and area at Karumba (northern Queensland) over a 16-year period, Oct 1994–Oct 2009 inclusive (mean, SE). For biomass, bold line is total, dashed lines represent the two main species *Halodule uninervis* (upper line) and *Halophila ovalis* (lower line). From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

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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).

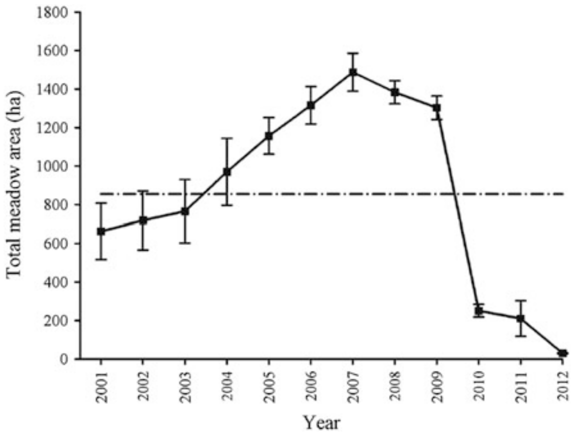

Fig. 7.2 Dynamic change in area of seagrass meadows in Cairns harbour (northern Queensland), over a 12-year period, 2001–2012 (mean, SE). Dashed line represents long-term mean. From McKenna et al. (2015). Major La Niña-related weather event occurred 2010/2011

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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

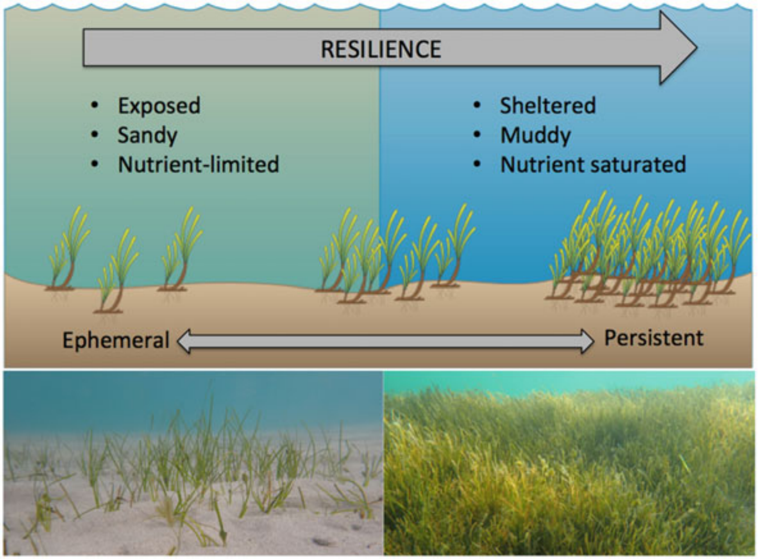

Fig. 7.3 Dynamics of seagrass populations vary among locations for *Heterozostera nigricaulis* in Port Phillip Bay. Populations living in sandy, nutrient-limited environments are more ephemeral and have little tolerance to nutrient and sediment stress, whereas populations in muddy, nutrient-saturated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

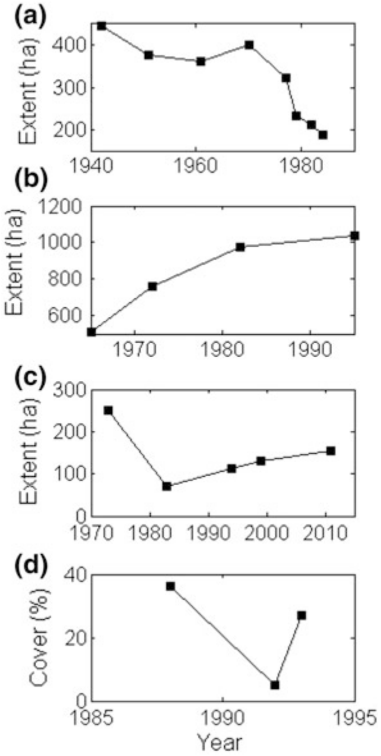

Fig. 7.4 Examples of population dynamics of seagrass in Australia: **a** *Posidonia australis*, Southern Shore, Botany Bay, NSW (redrawn based on data from Larkum and West 1990); **b** *Posidonia coriacea*, *Amphibolis griffithii*, Success Bank, WA (redrawn from Kendrick et al. 2000); **c** *Heterozostera 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

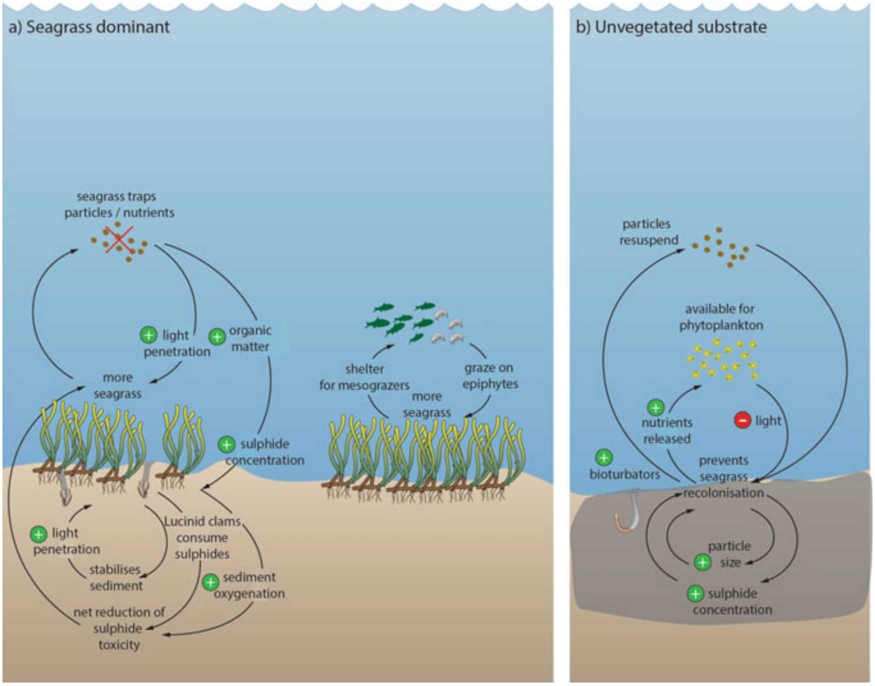

Fig. 7.5 Examples of feedback loops in seagrass ecosystems that mitigate the relationship between changing levels of environmental stress (disturbance) and the response of seagrass, in: **a** seagrass dominant habitat, and **b** unvegetated substrate (from Maxwell et al. 2017)

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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