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The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review

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ABSTRACT

Seagrass meadows are vital ecosystems in coastal zones worldwide, but are also under global threat. One of the major hurdles restricting the success of seagrass conservation and restoration is our limited understanding of ecological feedback mechanisms. In these ecosystems, multiple, self-reinforcing feedbacks can undermine conservation efforts by masking environmental impacts until the decline is precipitous, or alternatively they can inhibit seagrass recovery in spite of restoration efforts. However, no clear framework yet exists for identifying or dealing with feedbacks to improve the management of seagrass ecosystems. Here we review the causes and consequences of multiple feedbacks between seagrass and biotic and/or abiotic processes. We demonstrate how feedbacks have the potential to impose or reinforce regimes of either seagrass dominance or unvegetated substrate, and how the strength and importance of these feedbacks vary across environmental gradients. Although a myriad of feedbacks have now been identified, the co-occurrence and likely interaction among feedbacks has largely been overlooked to date due to difficulties in analysis and detection. Here we take a fundamental step forward by modelling the interactions among two distinct above- and belowground feedbacks to demonstrate that interacting feedbacks are likely to be important for ecosystem resilience. On this basis, we propose a five-step adaptive management plan to address feedback dynamics for effective conservation and restoration strategies. The management plan provides guidance to aid in the identification and prioritisation of likely feedbacks in different seagrass ecosystems.

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CONTENTS

I. INTRODUCTION

Coastal ecosystems constitute some of the most diverse and productive environments on Earth (Duarte & Chiscano, 1999). As a consequence, a majority of the human population lives along coasts drawing benefits from ecosystem services such as the provisioning of food, support of high primary productivity and biodiversity, and recreational and aesthetic services (MEA, 2005). However, centuries of unregulated resource use and transformation of coastal areas to suit human needs have degraded the resources, jeopardising future human development (Lotze *et al.,* 2006; Worm *et al.,* 2006). For a long time, coastal environmental management was typically based on the assumption of simple and linear relationships between causes (stressors) and effects (degradation) that could be predictably managed. However since the mid 20th century an increasing number of 'sudden', 'unexpected' and 'catastrophic' ecosystem shifts to undesirable and often apparently irreversible states has challenged traditional approaches to managing coastal resources (Barbier *et al.,* 2008; Duarte *et al.,* 2009; Kemp *et al.,* 2009; Carstensen *et al.,* 2011*b*).

In cold temperate to tropical shallow coastal zones worldwide, seagrass meadows are an integral part of coastal communities, supporting, regulating and providing high-value ecosystem services including productive fisheries (Unsworth *et al.,* 2010), nutrient cycling (McGlathery, Sundbäck & Anderson, 2007) and coastline stabilisation (Barbier *et al.,* 2008; Christianen *et al.,* 2013). Seagrass meadows sequester carbon and represent globally important 'blue carbon stocks' (Fourqurean *et al.,* 2012; Duarte *et al.,* 2013), and provide important sources of livelihoods and animal protein to coastal communities (Cullen-Unsworth *et al.,* 2014; de la Torre-Castro, Di Carlo & Jiddawi, 2014). However, like many coastal ecosystems, global areal coverage

of seagrass meadows is in decline, seagrass loss rates are increasing (Waycott *et al.,* 2009) and seagrass resilience needs closer management (Unsworth *et al.,* 2015). This is due to a range of pressures including declining water quality from increased coastal inputs of sediments and nutrients (Burkholder, Tomasko & Touchette, 2007; Boström *et al.,* 2014), extreme weather events such as cyclones and floods, the cascading effects from the loss of top-down control on seagrass epiphytes and drifting algae due to overfishing (Orth *et al.,* 2006; Baden *et al.,* 2010) and marine heat waves (Seddon, Connolly & Edyvane, 2000; Orth, McGlathery & Cole, 2012*a*; Fraser *et al.,* 2014; Thomson *et al.,* 2014). As seagrass meadows support a diverse range of organisms disproportionate to their area (Heck, Hays & Orth, 2003), ongoing degradation results in an impact greater than the loss of meadows alone.

The response of seagrass ecosystems to increasing pressures is determined by a diversity of concurrent interactions between the seagrass plants, the associated community of microbes, algae and animals, and the physical environment (de Boer, 2007; van der Heide *et al.,* 2007; Suding & Hobbs, 2009; Eklöf *et al.,* 2011, 2012; Carr *et al.,* 2012*a*). Seagrasses are archetypical ecosystem engineers (*sensu* Jones, Lawton & Shachak, 1994), exerting a strong influence over the environmental conditions, which can be necessary for their persistence in many cases (Gutiérrez *et al.,* 2011). The interactions between seagrass and local environmental conditions can result in non-linear relationships between increasing pressure and ecosystem responses (van der Heide *et al.,* 2007; Barbier *et al.,* 2008; Duarte *et al.,* 2009; Kemp *et al.,* 2009). In turn, non-linear relationships can result in hysteresis (Beisner, Haydon & Cuddington, 2003) in both seagrass degradation and recovery (Nyström *et al.,* 2012; McGlathery *et al.,* 2013). This often confounds a clear understanding of

the causal mechanisms behind ecosystem dynamics and also limits successful restoration efforts (Suding, Gross & Houseman, 2004).

Similar to many other marine systems, feedback mechanisms or 'feedback loops' play a major role in non-linear responses of seagrass meadows to environmental change (Nyström *et al.*, 2012). A feedback occurs when the current value of a state variable directly or indirectly affects the direction and rate at which that same variable changes (e.g. Meadows, 2008). Feedbacks can be positive, i.e. self-amplifying: for example, by trapping sediment, dense seagrass meadows can have a positive effect on light availability and thus benefit seagrass growth rate, driving further increase in seagrass density. Alternatively, feedbacks can also be negative, i.e. self-dampening: for example, high seagrass density can increase organic sediment loading, enhancing sulphide production, with adverse impact on seagrass density. Hence, positive and negative feedback mechanisms can stabilise and destabilise ecosystems, which create the potential for alternative and potentially stable states (Scheffer *et al.*, 2001).

Feedbacks can mitigate the direct effect of fluctuations in environmental conditions and system state (Walker *et al.*, 2004), and thus can mask the impact of deteriorating environmental conditions, such that minimum ecosystem response is observed until the capacity of stabilising feedbacks is overwhelmed and a change in state occurs (Scheffer *et al.*, 2001; Steffen *et al.*, 2004; Duarte *et al.*, 2009). In seagrass meadows, feedbacks have been found strongly to influence the trajectory between three distinct states or regimes (RSDB, 2015); (*i*) seagrass dominance, (*ii*) algal dominance (Duarte, 1995; Viaroli *et al.*, 2008) and (*iii*) unvegetated sediment (van der Heide *et al.*, 2007). Although many theoretical and small-scale experimental studies suggest that strong feedbacks may result in alternative stable states (e.g. van der Heide *et al.*, 2007, 2010*a*,*b*; Carr *et al.*, 2010), ecosystem-scale tests for true bi- or multistability in seagrass meadows or other ecosystems remain limited at present. Mounting evidence, however, demonstrates that feedback mechanisms are important drivers of ecosystem dynamics regardless of whether they result in truly persistent alternative equilibria, boom-and-bust cycles (van Nes, Rip & Scheffer, 2007) or more gradual but non-linear ecosystem responses to change (see e.g. Nyström *et al.*, 2012). In fact, the inherent complexity of ecosystems influenced by strong feedbacks has been suggested to pose one of the largest challenges for conservation and restoration (Suding *et al.*, 2004; Suykerbuyk *et al.*, 2012).

Herein we review the causes and consequences of multiple feedback mechanisms in seagrass ecosystems. First, we provide a comprehensive overview of 17 individual feedback mechanisms identified in seagrass ecosystems (Table 1, see online Appendix S1) with the aim to provide guidance for ecologists and managers. Next, we highlight that identification and management of feedbacks requires an ecosystem perspective, acknowledging that feedback mechanisms involve interactions among the seagrass plants themselves, associated organisms and the physical environment. We also show that the influence of feedbacks is likely to be strongly site-specific, scale-dependent, and dependent upon the morphological and life-history traits of dominant seagrass species and the nature and gradients of prevailing environmental conditions. Finally, we use a simple mathematical model to investigate how multiple, interacting feedbacks may potentially further complicate non-linear dynamics and bi- or multistability in seagrass ecosystems. On this basis we propose a decision-making framework to account for feedbacks in conserving and restoring seagrass ecosystems.

II. EXAMPLES OF THE INFLUENCE OF IMPORTANT FEEDBACKS IN SEAGRASS ECOSYSTEMS

In both seagrass meadows and ecosystems in general, a plethora of feedback mechanisms has been documented. Although is has been suggested that these feedbacks can co-occur and that their combined effects or interactions may affect ecosystem dynamics and responses to environmental change (e.g. Scheffer *et al.*, 2001; Nyström *et al.*, 2012; van de Leemput *et al.*, 2016), the vast majority of studies have focused on individual feedbacks. Consequently, we review and summarise knowledge on individual feedbacks in seagrass ecosystems.

Feedbacks between seagrass, other organisms and abiotic conditions can be important for the stability and resilience of seagrass ecosystems. Hence disruptions of feedbacks can modify the structure and functioning of seagrass ecosystems, thus also changing the flow of services to society. Moreover, the loss of seagrass can impact all trophic levels, due to feedbacks and interactions between seagrass and local environmental conditions (Gutiérrez *et al.*, 2011). The best-documented example is how seagrass shoot density, in interaction with the spatial extent of a meadow, affects water movement (Fig. 1A, Table 1). These effects have been investigated in numerous studies across multiple species and under a wide range of laboratory and field conditions (Gambi, Nowell & Jumars, 1990; Bos & van Katwijk, 2007). Seagrass leaves and shoots slow water flow though the meadow canopy (Hansen & Reidenbach, 2012), protecting other leaves from the physical stress of water drag (Fonseca *et al.*, 1982; Fonseca & Cahalan, 1992) and trapping suspended particles from the water column (Hendriks *et al.*, 2008, 2010), thereby increasing light penetration and improving conditions for seagrass growth (Fonseca & Fisher, 1986; van der Heide *et al.*, 2007; Carr *et al.*, 2010; Yang, HilleRisLambers & Ruesink, 2016). Sediment resuspension is reduced by the seagrass leaves and the network of roots and rhizomes, which further stabilise the sea floor and improve the light climate for seagrasses (Fig. 1A) (Terrados & Duarte, 2000; Gacia *et al.*, 2003; Christianen *et al.*, 2013). As sediments outside the meadow remain unbound and more susceptible to erosion, this process results in the sediments within the meadow becoming progressively muddier than sediments

Table 1. Feedback mechanisms known to occur in seagrass ecosystems (for further details see online Appendix S1). Green indicates self-amplifying feedbacks, whereby increase in seagrass density generates conditions which promote further increase in density, until carrying capacity is reached or poor environmental conditions overwhelm the feedback. Red indicates self-dampening feedbacks, whereby increase in seagrass presence creates conditions adverse to seagrass, such that seagrass subsequently declines. Yellow indicates feedbacks, which can be both self-amplifying and self-dampening.

	Feedback name	Feedback description	Operates under following conditions and scale:			
			Climate	Hydrodynamics	Nutrient state	Spatial scale
1	Sediment trapping	Seagrass traps water column sediment, improving water clarity, seagrass growth, and seagrass depth range (e.g. de Boer, 2007; Carr *et al.*, 2010, 2012*a,b*; Hansen & Reidenbach, 2012; Lawson *et al.*, 2012).	All	(Semi-)exposed	All	~1–>100 m
2	Erosion-facilitated spatial patterning	Interacting positive and negative feedbacks of erosion/sediment trapping acting at small and larger scales lead to self-organised pattern (e.g. van der Heide *et al.*, 2010*a*)	Observed in temperate ecosystems	Exposed	All	~1–~10 m
3	Reduced intertidal desiccation	High-density seagrass reduces desiccation in intertidal areas, creating more favourable seagrass growth conditions higher in intertidal zone (e.g. Fox, 1996; Tsai *et al.*, 2010)	All, but drought stress increases with temperature	All	All	~1–~10 m
4	Ammonium uptake	High-density seagrass takes up more ammonium, reducing toxicity, favouring seagrass growth (e.g. McGlathery *et al.*, 2007, 2012; van der Heide *et al.*, 2010*b*; Cole & McGlathery, 2012)	All	Sheltered	Eutrophic	~10–>100 m
5	Hydrodynamic disruption	High-density seagrass reduces near-bed water currents, reducing physical stress on seagrass plants and stabilising sediments. Small seagrass patches or meadow edges may increase turbulence locally resulting in erosion and scouring (e.g. Fonseca & Koehl, 2006; Bos & van Katwijk, 2007; Infantes *et al.*, 2009; van Katwijk *et al.*, 2010)	All	Exposed	All	<1–>100 m
6	Changing sediment size	High-density seagrass captures fine material, sediments become muddier. In small low-density patches, sediments can become more sandy (e.g. Bouma *et al.*, 2009; van Katwijk *et al.*, 2010; McGlathery *et al.*, 2012)	All	(Semi-)exposed	All	<1–>100 m
7	Sediment sulphide toxicity	High-density seagrass traps organic matter which decomposes, leading to sulphide toxicity which impairs seagrass growth (e.g. Folmer *et al.*, 2012; van der Heide *et al.*, 2012*b*)	All, but increases with temperature	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1–10 mm
8	Sediment oxygenation	High-density seagrass, or multiple seagrass species in mixed meadows, oxygenates sediments reducing sulphide concentration, thus improving sediment conditions for seagrass growth (e.g. Borum *et al.*, 2005; Mascaro *et al.*, 2009; Brodersen *et al.*, 2014)	All, but increases with temperature	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1–10 mm
9	Lucinidae presence	Mutualistic feedback in which lucinid bivalves alleviate negative feedback by consuming toxic sulphide (see mechanism 6), while seagrass provides lucinids with oxygen (van der Heide *et al.*, 2012*b*; de Fouw *et al.*, 2016)	(Sub-)tropical	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1–10 mm
10	pH toxicity	Photosynthesis leads to elevated pH which inhibits seagrass growth (e.g. Beer *et al.*, 2006)	All	Sheltered	All	~1–>100 m

Table 1. continued

|	Feedback name	Feedback description	Operates under following conditions and scale:			
			Climate	Hydrodynamics	Nutrient state	Spatial scale
11	Carbonate dissolution	High density of seagrass generates CO_2 by enhancing aerobic organic matter mineralisation, increasing levels of calcium carbonates and phosphates, and increasing P availability and thus increases seagrass growth (Marbà *et al.*, 2006; Burdige, Zimmerman & Hu, 2008; Long *et al.*, 2008)	(Sub-)tropical	Semi-exposed to sheltered	Oligotrophic	~1 – 10 mm
12	Genetic diversity	Meadows with high genetic diversity and connectivity between regions show increased community-level persistence against disturbance (e.g. Williams & Heck, 2001; Hughes & Stachowicz, 2004; Procaccini, Olsen & Reusch, 2007; Reynolds, Waycott & McGlathery, 2013)	All	All	All	> 1 km
13	Mesograzer habitat	Seagrass shelters mesograzers from predation, increasing epiphyte grazing, improving light availability and seagrass growth (e.g. Schanz & Asmus, 2003; Valentine & Duffy, 2006; Duffy *et al.*, 2015)	All	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1 –> 100 m
14	Juvenile predator habitat	Seagrass shelters juveniles of large predators which as adults control smaller predator density, leading to more mesograzers (e.g. Valentine & Duffy, 2006; Eriksson *et al.*, 2011)	All	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1 –> 100 m
15	Megaherbivore-induced nutrient tolerance	High seagrass biomass attracts megagrazers (e.g. turtles, dugongs) whose grazing activities alleviate the negative effects of eutrophication by stimulating seagrass production (e.g. Christianen *et al.*, 2012)	(Sub-)tropical	Semi-exposed to sheltered	Mesotrophic to eutrophic	~1 –> 100 m
16	Megaherbivores overgrazing	Overgrazing by megaherbivores drives adverse feedbacks and prevents seagrass recovery. Seagrass decline increases grazing pressure on remaining meadows (e.g. Christianen *et al.*, 2014)	(Sub-)tropical	(Semi-)exposed	All	~1 –> 100 m
17	Sea urchins: grazing	Overgrazing of seagrass by sea urchins reduces seagrass aboveground biomass which leads to increased predation pressure on sea urchins, through the loss of shelter, leading to reduced urchins and recovery of seagrass density (e.g. Heck & Valentine, 1995)	(Sub-)tropical	All	All	~1 –> 100 m
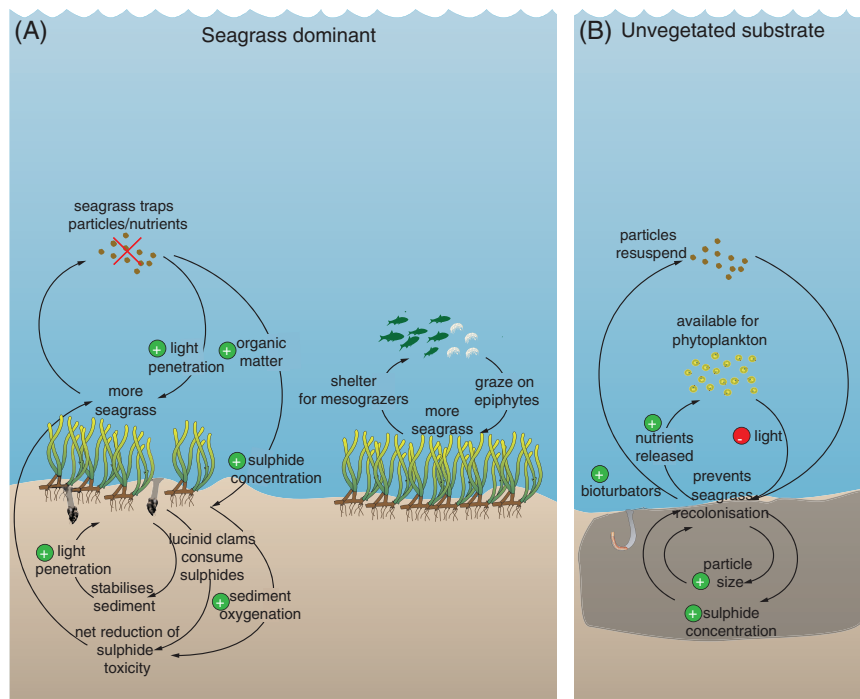
Fig. 1. Feedback loops in seagrass ecosystems that control the stability of alternate regimes. (A) Seagrass dominant; (B) unvegetated. + (Green) symbols indicate an increase and − (red) symbols indicate a decrease in levels.

outside (Bos & van Katwijk, 2007; van der Heide *et al.*, 2007, 2011; McGlathery *et al.*, 2012). On the other hand, single shoots, patches or meadow edges form obstacles to tidal flow, locally increasing turbulence (Verduin & Backhaus, 2000; Fonseca & Koehl, 2006; Backhaus & Verduin, 2008; Luhar, Rominger & Nepf, 2008; Plew, Cooper & Callaghan, 2008; Bouma *et al.*, 2009). Consequently, meadow edges are prone to local erosion (Bouma *et al.*, 2009) and often have coarser sediments than adjacent bare areas, while low-density beds can become sandier by losing fine particles (van Katwijk *et al.*, 2010). In some cases, such erosion processes can even limit the size of patches and cause self-organised spatial patterns through the interactions of feedbacks at different scales (Fonseca, Zieman & Thayer, 1983; Fonseca & Bell, 1998; van der Heide *et al.*, 2010*a*).

The physical disruption of water flow over seagrass meadows also traps and deposits organic matter, which when broken down at low concentrations (Heiss, Smith & Probert, 2000), can improve plant productivity especially in oligotrophic seagrass ecosystems (McGlathery *et al.*, 2007). At higher concentrations, however, the decomposition of organic material can lead to sulphide toxicity in the sediments which can impair seagrass shoot density, rhizome extension (van der Heide *et al.*, 2012*b*) and growth in locations where seagrass has been lost (Fig. 1B) (Holmer *et al.*, 2009; Mascaro *et al.*, 2009; Folmer *et al.*, 2012). Seagrass meadows can alleviate the toxic effect of sulphide build-up by oxygenating the sediments adjacent to the rhizome surface (Borum *et al.*, 2005; Mascaro *et al.*, 2009; Brodersen *et al.*, 2014), but oxygen transport can only occur under favourable conditions for

photosynthesis (Borum *et al.*, 2006) so the rate of flow of oxygenated water across the plants in dark periods is also important in hypoxia (Pedersen *et al.*, 2016).

The feedbacks described above all involve interactions between seagrass plants and abiotic conditions, however a growing number of examples show the importance of positive interactions between meadows and the organisms they support. The importance of multiple-species feedback control is highlighted by a three-stage mutualistic feedback between seagrass, lucinid bivalves and their endosymbiotic sulphide-oxidizing bacteria. This association occurs in many seagrass meadows worldwide, and has been shown to be a key factor determining ecosystem functioning in the intertidal seagrass beds of Banc d'Arguin (West Africa), and potentially in other subtropical to tropical, organic matter-rich systems (Folmer *et al.*, 2012; van der Heide *et al.*, 2012*b*; Govers *et al.*, 2014). In those systems, seagrass production can become enhanced by mutualism as the lucinid bivalves and their gill bacteria reduce sulphide levels (Fig. 1A) (van der Heide *et al.*, 2012*b*; de Fouw *et al.*, 2016). This relationship also has benefits for the bivalves, which thrive in the accumulated organic matter and profit from radial oxygen release from seagrass roots.

Seagrass ecosystems are also vulnerable to competition for light from other primary producers including phytoplankton (Viaroli *et al.*, 2008), epiphytic micro- and macroalgae (Lapointe, Tomasko & Matzie, 1994) and floating macroalgae (Hauxwell *et al.*, 2001). Floating algae mats are highly variable in their spatial and temporal distribution, with aggregations of algal mats dependent upon the hydrological

regime present (e.g. water currents and wave action) (Bell & Hall, 1997). Aboveground structure and reduced water velocity within seagrass meadows tend to cause algae mats to accumulate within the meadows (Rasmussen *et al.*, 2013). The vulnerability of seagrass meadows to competition from algae is partially reduced by a complex suite of interacting feedbacks between the seagrass plant, water-column nutrient concentrations, the abundance of mesograzers feeding on the algae, and the top-down control of predator abundance (Hays, 2005), which ultimately create a feedback between seagrass presence and/or abundance and water clarity (Fig. 1A). The seagrass canopy provides significant predation shelter for mesograzers (e.g. gastropods, amphipods, isopods and herbivorous fish) which graze on seagrass epiphytes and opportunistic macroalgae (Baden *et al.*, 2012). The resultant positive effect on seagrass production is complemented by the uptake of water-column nitrogen by seagrass leaves (Pedersen & Borum, 1993) and the bacterial communities associated with the meadow (McGlathery *et al.*, 2007). In relatively eutrophic areas, this allows seagrass meadows to withstand relatively high nutrient loads if the shoot density of the meadow is sufficiently high (Webster & Harris, 2004; van der Heide *et al.*, 2010*b*).

Feedbacks involving grazers can have a range of impacts on seagrass ecosystems. In tropical regions, higher shoot density attracts megagrazers (e.g. turtles and dugongs) whose grazing on seagrasses reduces the effects of eutrophication by stimulating seagrass production and nutrient export (Christianen *et al.*, 2012). Hence, harvesting of megagrazers can also adversely affect seagrass, by inhibiting mitigation of eutrophication and sea urchin outbreaks (Christianen *et al.*, 2012). However, overgrazing of seagrass meadows by sea turtles (Christianen *et al.*, 2014) or other grazers such as sea urchins (Eklöf *et al.*, 2008) can also pose a threat to seagrass ecosystems. Therefore, over-fishing of large predators such as sharks (Valentine & Duffy, 2006) can cause proliferation of seagrass grazers to excessive levels (Eklöf *et al.*, 2009; Christianen *et al.*, 2014; Heithaus *et al.*, 2014). Similarly, removal of top predators has also been found to cascade down multiple trophic levels by releasing small predators that in turn depress the stabilising influence of algae-removing mesograzers (Munkes, 2005; Moksnes *et al.*, 2008; Baden *et al.*, 2012; Hughes *et al.*, 2013).

III. CHANGES IN RELATIVE IMPORTANCE OF FEEDBACKS ALONG ENVIRONMENTAL STRESS GRADIENTS

The ability of ecosystems to withstand environmental stress depends on the magnitude and diversity of tolerance levels of individual organisms, and on the ability of organisms to buffer stressors by modifying the environment (DeAngelis, Post & Travis, 1986; Bruno, Stachowicz & Bertness, 2003; Elmqvist *et al.*, 2003; Schröder, Persson & De Roos, 2005). Depending on the types of feedbacks involved, the capacity of seagrass ecosystems to mitigate environmental stress is

typically both density- and scale-dependent (see Table 1). Habitat modification by seagrass productivity therefore creates a feedback, in which seagrass creates conditions which promote further seagrass growth. In turn, this implies that seagrass meadows may be able to buffer environmental stress to a certain level, but that the capacity of feedbacks to stabilise the ecosystem may be lost beyond this threshold, resulting in ecosystem degradation which may be difficult to reverse (Scheffer *et al.*, 2001; van der Heide *et al.*, 2007; Carr *et al.*, 2010).

Increased nutrient loading, especially when combined with slow water exchange rates in sheltered conditions (i.e. long residence times), causes a shift from long-lived and slow-growing rooted seagrasses to fast-growing macroalgae and phytoplankton dominance (Duarte, 1995; Valiela *et al.*, 1997). The dominance of macroalgae or phytoplankton under high nutrient loading is potentially determined by water residence time (Valiela *et al.*, 1997), with shorter residence times favouring macroalgal dominance. The transition between the different states is often abrupt, occurring rapidly once the capability of feedbacks to buffer environmental stress is exceeded. In oligotrophic waters, seagrass growth is often stimulated by nutrients originating from organic particles trapped by the canopy and decomposing in the meadow (Fig. 2A) (McGlathery *et al.*, 2007, 2012). Because sediment trapping depends on the aboveground meadow traits (e.g. length and density of shoots), the strength of feedbacks between seagrass meadows and light climate is also likely to vary between species (see below discussion of wave attenuation).

The retention of nutrients in shallow coastal seagrass meadows has been shown to occur even when nutrient loadings are relatively high for much of the year (Valiela *et al.*, 1997; McGlathery, Sundback & Anderson, 2004). Maintaining water clarity and low phytoplankton biomass will depend on both nutrient loading and the degree to which the meadow is able to modify its environment (i.e. the strength of the feedback). When nutrient availability exceeds the sum of the growth requirements and storage capacity of the seagrass meadow, excess nutrients accumulated in the meadows may promote proliferation of opportunistic algae, ultimately causing a regime shift away from seagrass dominance (Webster & Harris, 2004). As a consequence, the nutrient retention feedback is strongest at low to intermediate nutrient levels (McGlathery *et al.*, 2007).

At low to intermediate levels of nutrient loading, grazers may buffer any adverse effects of enrichment, with latitudinal differences likely dictating the type and relative strength of this feedback (e.g. Poore *et al.*, 2012). In tropical regions, direct seagrass grazing by large megaherbivores like sea turtles alleviates the negative effects of eutrophication through the stimulation of seagrass production (Christianen *et al.*, 2012). In temperate regions and tropical regions, herbivorous mesograzers (crustaceans, gastropods) and filter-feeding bivalves can mitigate negative impacts of nutrient loading by consuming algae and channelling carbon and nutrients to higher trophic levels (Duarte, 1995; Hay
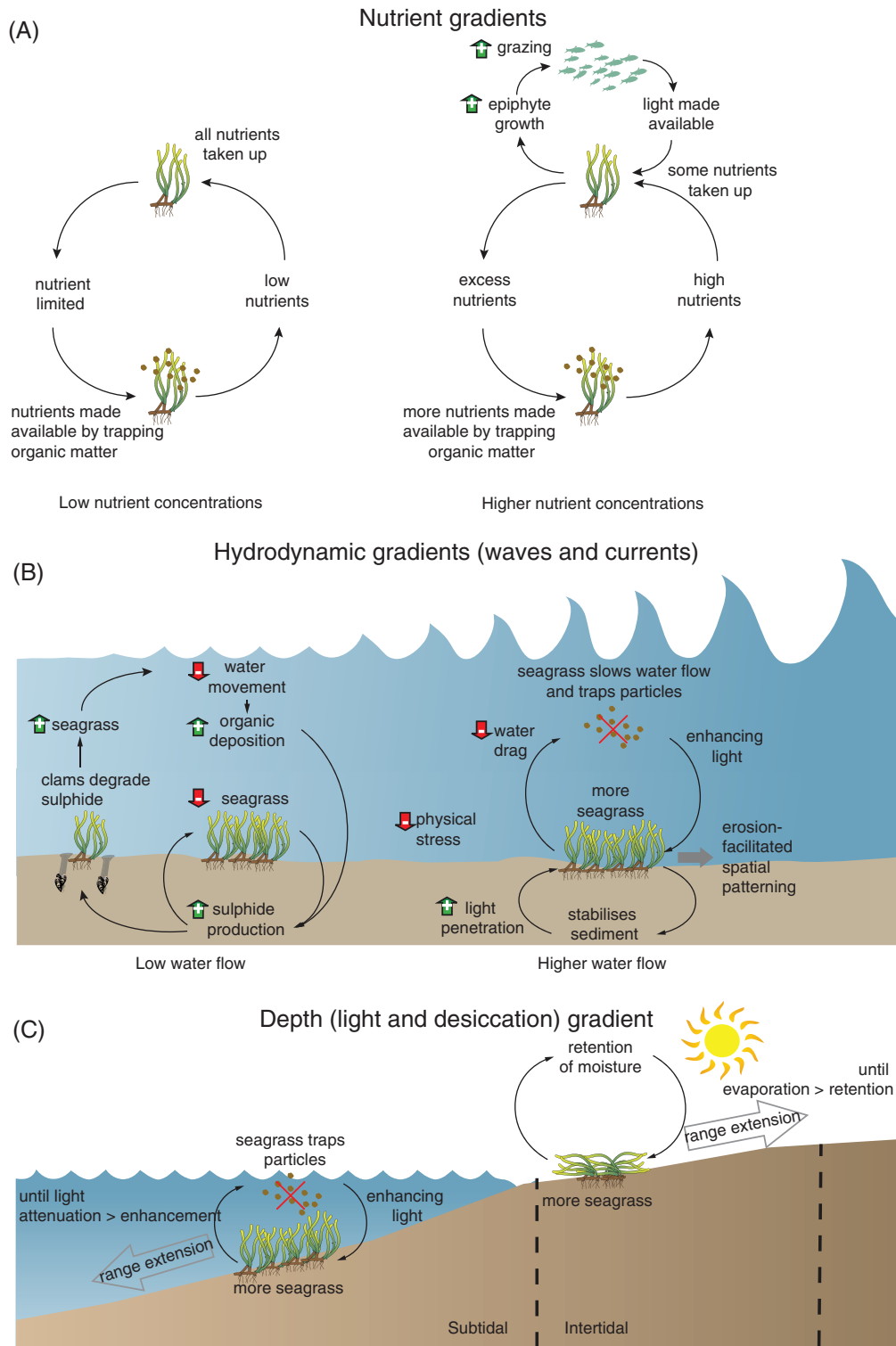
Fig. 2. Variation in feedback processes across environmental gradients. (A) When nutrient limited, seagrass meadows quickly sequester any nutrients from the water column, lowering their availability to seagrass competitors. When the system is eutrophied, more nutrients are available for algal growth. Excess algal growth is controlled by algal grazers, which in turn have a positive effect on seagrass growth. (B) Changes to the hydrodynamics of the meadow can affect sediment toxicity and stability, which in turn affects seagrass persistence. + (Green) symbols indicate an increase and − (red) symbols indicate a decrease in levels. (C) The ability of seagrass meadows to trap particles and improve light varies along the depth gradient.

et al., 2004; Duffy *et al.,* 2015). Meanwhile, these herbivores typically benefit from the presence of canopy-forming plants like seagrasses, which provide shelter from visual predators (Heck & Valentine, 2007). Excessive nutrient loads, however, can exceed the capacity of grazing feedbacks (Carruthers, van Tussenbroek & Dennison, 2005). In such cases, grazing rates become saturated, causing a proliferation of fast-growing macroalgae, epiphytic algae and phytoplankton (Duarte, 1995). These changes can ultimately reduce grazer abundance, for example if eutrophication causes hypoxia or anoxia (Hauxwell *et al.,* 1998), indirectly increasing algal biomass even further.

The effect of seagrass meadows on water flow attenuation varies with both plant traits and the level of stress (hydrodynamic forcing) (Fig. 2B). In areas with limited water movement (e.g. in semi-closed estuaries or shallow, well-protected embayments), external nutrient loading and/or build-up of organic matter may lead to toxic levels of sulphide in the sediment and high ammonium concentrations in the water layer and the sediment (van Katwijk *et al.,* 1997; Lee & Dunton, 2000; Touchette & Burkholder, 2000). To a certain level, toxicity effects of ammonium can be prevented by rapid uptake at high seagrass densities, whereas sulphide toxicity can be mediated by radial oxygen loss from the dense root mat (van der Heide *et al.,* 2008, 2010*b*). Sulphide accumulation in warmer regions can be mitigated by a tripartite mutualism between seagrass, lucinid bivalves and their endosymbiotic sulphide-reducing gill bacteria in systems with sufficient abundance of bivalves (Fig. 2A) (van der Heide *et al.,* 2012*b*; de Fouw *et al.,* 2016). Additionally, sulphide oxidation can be facilitated by microbial mediation (Jørgensen & Revsbech, 1983) which is enhanced by oxygen release from root and rhizome tissues (Caffrey & Kemp, 1991).

In areas with moderate hydrodynamic energy, the seagrass canopy reduces water-flow rates, which in turn reduces sediment resuspension and creates a calm microclimate favouring seagrass growth and recruitment of new individuals. These effects also depend on meadow characteristics like shoot density and patch size (e.g. Bos *et al.,* 2007). At low shoot densities or patch sizes, seagrass may have very little stabilising capacity and may even enhance local resuspension (Lawson, McGlathery & Wiberg, 2012). In high-energy environments, however, hydrodynamic forcing typically exceeds the flow-attenuating capacity of most seagrasses, with the exception of species strongly reinforced with fibrous aboveground tissues like *Amphibolus giffithii* (Carruthers *et al.,* 2007), and results in conditions that are unfavourable for seagrasses; e.g. continuous sediment resuspension and high turbidity, lack of stable sediments for seedling growth, and strong wave action that damages or uproots plants. Seasonal variation in wave energy can result in variation in sedimentation rates within the meadow with deposition occurring in calmer months (e.g. Carruthers *et al.,* 2007) and significant scouring occurring in periods of higher wave energy (e.g. van Keulen & Borowitzka, 2003).

Seagrass feedbacks also affect the minimum and maximum depth limits of many seagrass meadows. At the landward meadow edge in intertidal areas, desiccation during low tides limits the extent of seagrass meadows (Bjork *et al.,* 1999). However, seagrass persistence is here enhanced by a positive feedback between seagrass aboveground biomass and water retention. When exposed to air, seagrass leaves trap and retain a layer of water, which in turn maintains leaf moisture content and photosynthesis (Leuschner, Landwehr & Mehlig, 1998; Silva *et al.,* 2005). This self-facilitation enables seagrass persistence and expansion in the intertidal zone, particularly for meadows with high shoot and leaf density (Bjork *et al.,* 1999; Silva & Santos, 2003). Range expansion under these conditions is, however, limited once the rate of evaporation due to exposure is greater than the moisture retention capacity of the meadow (Fig. 2C) (Shafer, Sherman & Wyllie-Echeverria, 2007). The ability of the feedback to buffer desiccation stress will therefore fluctuate with season and tidal regime, and can result in 'sudden' die-offs of shallow meadows when stress levels (time of exposure, air and water temperature) exceed the buffering capacity of the feedback (Seddon *et al.,* 2000; Thomson *et al.,* 2014).

At the deep edge of the meadow, the maximum seagrass depth limit is controlled by irradiance (Dennison & Alberte, 1985), which is a function of water clarity (Abal & Dennison, 1996), which can be affected by the ability of seagrasses to trap particles, stabilise sediment and take up nutrients (Fig. 2C). The strength of these feedbacks therefore affects seagrass range expansion into deeper waters.

IV. ADDRESSING THE COMPLEXITY OF MULTIPLE AND INTERACTING FEEDBACKS

Above we outlined the range of individual feedback processes that have been described in seagrass meadows. Each of these feedbacks alone can influence the resilience of seagrass ecosystems. In reality, however, multiple feedbacks are likely to act simultaneously, with the relative importance of each of these in shaping the ecosystem depending on the environmental setting. For instance, in more-sheltered conditions, nutrient uptake and sulphide-detoxification feedbacks are likely to be relatively important (van der Heide *et al.,* 2010*b*, 2012*a*; Folmer *et al.,* 2012), whereas wave-attenuating, sediment-stabilising and particle-trapping feedbacks will increase in importance with increasing hydrodynamic exposure.

Multiple feedbacks may be important under the same environmental conditions but may shift in strength depending on the traits of the species/phenotype (Puijalon *et al.,* 2011) and level of stress. In many cases there is the potential for more than two stable states under the same external environmental conditions. For instance, an area with high environmental stress (e.g. wave action) may be dominated by a single species with a very high stress resistance or intermediate habitat-modifying properties (Fig. 3). As environmental stress gradually decreases, however, the area may potentially become suitable for multiple seagrass species that may dominate the system depending on the initial conditions – for
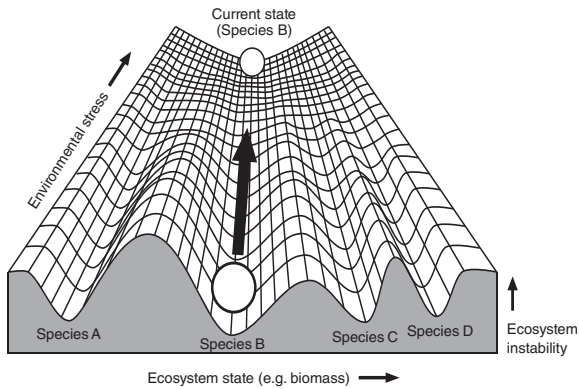
Fig. 3. Heuristic model depicting a landscape of multiple states dominated by different seagrass species depending on environmental stress (e.g. hydrodynamics) and initial conditions. At low environmental stress, four different states, each dominated by a different seagrass species (with increasing biomass from left to right) are possible depending on the initial conditions. However, as environmental stress increases, resilience of the states dominated by D, C and A, respectively, decreases, ultimately allowing only one possible state dominated by species B. Note that the deepest valley indicates the most stable state and that peaks depict unstable equilibria.

instance, species with lower resistance and/or weaker engineering properties (*sensu* Bouma *et al.*, 2005).

Multiple feedbacks in seagrass ecosystem may also interact. For instance, local positive feedbacks (e.g. increased protection from uprooting by improved anchoring with increased seagrass density) and long-range negative feedbacks (e.g. sediment erosion around seagrass shoots) have been demonstrated interactively to form seagrass meadows with highly regular spatial patterns (van der Heide *et al.*, 2010a). Furthermore, there is increasing evidence that multiple positive and negative feedbacks interact in food webs where mesograzers benefit seagrasses by reducing algal biomass (Fig. 4). Mesograzers can be controlled by intermediate predators such as invertivorous fish, crabs and shrimp (Moksnes *et al.*, 2008; Baden *et al.*, 2012), which in turn may be locally controlled by top predatory fish (Eriksson *et al.*, 2009) or sea otters (Hughes *et al.*, 2013). Importantly, both mesograzers and juveniles of large predatory fish may simultaneously benefit from the shelter provided by seagrass canopies (Pihl *et al.*, 2006; Lilley & Unsworth, 2014). If these reciprocal interactions are strong enough, trophic cascades from large predatory fish down to seagrass may, in fact, be part of a web of both positive and negative feedbacks (Fig. 4) that interactively determine seagrass ecosystem resilience to eutrophication (Valentine & Duffy, 2006). While the net effect of these interactions can sometimes be straightforward (Moksnes *et al.*, 2008), it will vary among systems and be influenced by factors such as the densities and traits of seagrasses, prey and predators (Scheinin *et al.*, 2011), and the degree to which different species benefit from seagrass compared with algae (Whalen, Duffy & Grace, 2013).

Finally, it appears likely that multiple positive feedbacks that occur simultaneously also interact in synergistic or
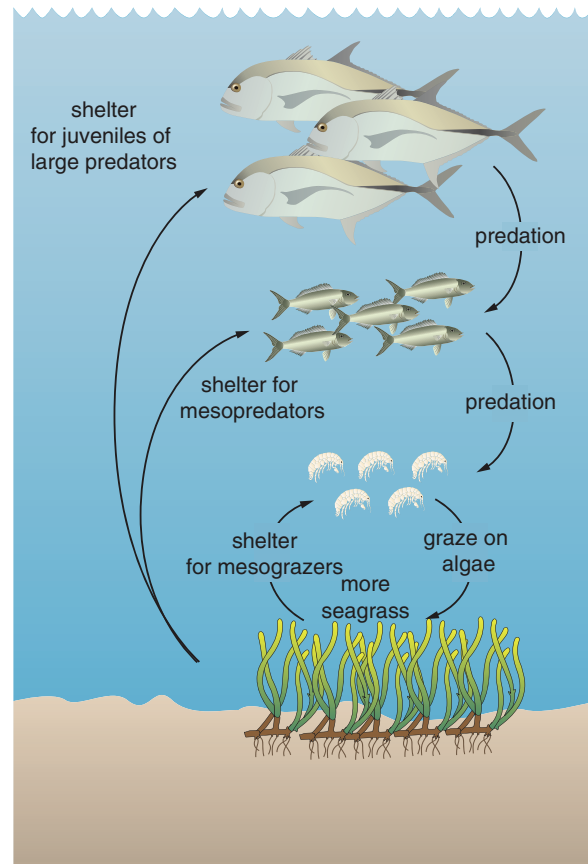

Fig. 4. Interacting trophic cascades and non-trophic interactions causing two intertwined feedbacks. In the first feedback, seagrass is facilitated by mesograzers through grazing of macroalgae and/or epiphytes growing on the seagrass leaves, while seagrass facilitates mesograzers by providing shelter. A second positive feedback occurs when large predatory fish indirectly facilitate seagrasses through mesopredator control, while seagrass facilitates large predatory fish by providing shelter (e.g. nursery habitat). In the trophic cascade, smaller predatory fish are predated by the larger fish, alleviating predation pressure on mesograzers, indirectly facilitating seagrasses through enhanced grazing on macroalgae and epiphytes.

antagonistic ways, increasing the complexity of seagrass ecosystem responses to environmental change. For example, in tropical coral reefs, single feedbacks may be too weak to trigger bistability, but when interacting and reinforcing each other, multiple feedbacks may together cause switches to alternative, stable states (van de Leemput *et al.*, 2016). To shed more light on the potential consequences of interacting feedbacks, we constructed a minimal model that includes two common seagrass feedback mechanisms: (*i*) a biophysical feedback that describes the attenuating effects of seagrasses on hydrodynamics with increasing biomass; and (*ii*) a biogeochemical mutualism-based feedback, in which increasing biomass of both seagrass and lucinid bivalves buffer against sulphide production from degradation of organic matter trapped by the seagrasses (see online Appendix S2). Next, we used the model to explore how

gradients in both eutrophication and hydrodynamics affect the interactions between both feedbacks and the net outcome for the system.

The model predictions suggest that lucinid biomass increases with eutrophication level and buffers against sulphide production, but can also cause alternative stable states (bistability) when eutrophication is high (Fig. 5A, B). Moreover, the thresholds for bistability along the eutrophication gradient shift depending on the hydrodynamic intensity. Finally, our model analyses demonstrates that the interaction between the biophysical and biogeochemical feedbacks can actually create multiple ranges of bistability as a direct consequence of the interaction between feedbacks along the hydrodynamic gradient (Fig. 5C). In other words, rather than having a 'classic' single range of hysteresis along the environmental gradient (hydrodynamics in our case), the interacting feedbacks create two separate ranges of alternative stable states. Thus the complexity of the seagrass ecosystem response to changes in hydrodynamic conditions may be much higher than previously thought – especially in warm regions where the mutualism feedback appears strongest. Albeit still at a theoretical stage, these results strongly suggest that consideration of the interactive and potentially synergistic effects of multiple feedback mechanisms in given environmental settings may be crucial for the protection of seagrass meadows and their services, as well as for the restoration of seagrass ecosystems already lost.

V. FEEDBACKS AND THE SUCCESS OF SEAGRASS CONSERVATION AND RESTORATION

Protection and conservation of seagrass meadows has traditionally focused on successional-based, passive approaches that assume that re-establishing the historical abiotic conditions that existed prior to degradation will return the ecosystem to its original state (Parker, 1997; Young, 2000; Suding *et al.*, 2004; Simenstad, Reed & Ford, 2005). Other more active approaches include seagrass planting and seeding efforts for successful restoration (Fonseca & Fisher, 1986; Cloern, 2001; Kenworthy *et al.*, 2006; Orth *et al.*, 2006, 2012*b*; Paling *et al.*, 2009; Estes *et al.*, 2011; Greening, Cross & Sherwood, 2011). However, natural recolonisation or assisted recovery following small-scale planting may be impossible or very slow when feedbacks have been disrupted (Suding *et al.*, 2004; Suykerbuyk *et al.*, 2012). Characterising feedback processes that influence the responses of seagrass ecosystems may help identify the conditions that prevent recovery and allow those to be addressed through additional targeted management action, thereby increasing management success (Suding *et al.*, 2004; Nyström *et al.*, 2012). While feedbacks are usually not directly considered in these programs, we suggest that management and monitoring of feedbacks is necessary as they directly affect seagrass ecosystem structure and functioning. Such a focus may improve the foundation
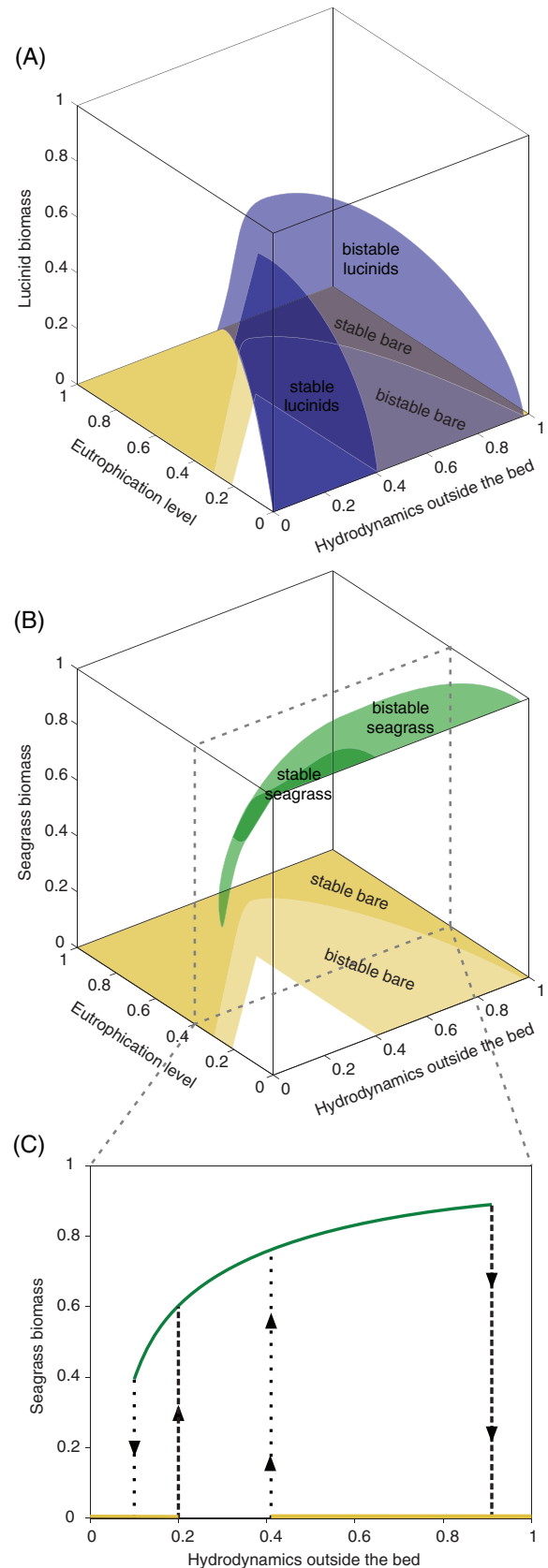
Fig. 5. Legend on Next page.

for management success by also directly targeting the processes that mediate the persistence of both desirable and unwanted regimes (Scheffer *et al.,* 2001; Folke *et al.,* 2004; Suding *et al.,* 2004; van Katwijk *et al.,* 2009, 2016; Maxwell *et al.,* 2015). Moreover, if rapid regime shifts are possible due to strong feedbacks, traditional measures used for monitoring, such as seagrass density, cover and areal extent may be misleading. These measures can still be very high when the system is close to collapse, thus supplementary indicators and novel approaches may be necessary (e.g. see Soissons *et al.,* 2014, and references therein). To help address this gap in management, we propose a five-step adaptive management process to incorporate knowledge of feedbacks in seagrass conservation and restoration (Fig. 6).

(1) Step 1: identify whether conservation and/or restoration is the goal of the program

Conserving seagrass ecosystems may require a focus on feedbacks different from those that impede the restoration of seagrass on unvegetated habitat (see step 3 below) and thus requires a different management framework.

(2) Step 2: identify feedbacks likely to affect conservation or restoration success

This step is based on the feedbacks outlined in Table 1 and see online Appendix S1. The key question to address in this step is: which influential feedback or set of feedbacks controls the resilience of the current and/or desired state of the seagrass ecosystem? In order to do that, there are three important elements to consider: (*i*) what are the

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Fig. 5. Explorative bifurcation analysis of the theoretical model described in online Appendix S2 (relatively scaled between 0 and 1). (A) Lucinid biomass increases in the seagrass meadow with an increasing eutrophication level as sulphide availability increases. (B) Hydrodynamics facilitates seagrass, enabling a healthy meadow to persist over a wide range of conditions, whereas colonisation of bare areas is often not possible (bistable areas). (C) Seagrass biomass at intermediate levels of eutrophication; bistability occurs twice along the hydrodynamic gradient. Seagrass growth is impossible near zero hydrodynamics due to high sulphide levels caused by excessive organic matter build-up. Limited flushing of organic matter by low hydrodynamics reduces sulphide sufficiently to allow two possible states: (*i*) a healthy seagrass system in which lucinids remove remaining sulphide and (*ii*) a bare system where spontaneous development of the seagrass–lucinid mutualism is impossible. When hydrodynamics are between ~0.2 and ~0.4, flushing of organic matter is sufficient to allow seagrass growth irrespective of initial conditions. When above 0.4, hydrodynamics are too strong to allow individual seagrass plants to survive, but a high-density meadow sufficiently reduces hydrodynamics inside the bed to allow it to persist. Above ~0.9, buffering of hydrodynamics by the meadow becomes insufficient and only a bare situation is possible. Arrows depict the direction of change at each respective bifurcation point.

pressures that might cause a feedback? (*ii*) Are those pressures increasing towards a presumed threshold that might lead to collapse (relevant for conservation), or prevent recovery (relevant for restoration)? (*iii*) What are the corresponding levels of key seagrass variables (e.g. seagrass density, cover, extent or biomass) and key process variables (e.g. grazing rates, sediment trapping, sediment toxicity reduction rates) required to support the desirable feedbacks according to the management goal?

(3) Step 3: take action to address feedbacks permanently or temporarily

To improve the likelihood of restoration success where recovery is inhibited by sediment–seagrass feedbacks, sediments can be stabilised through engineering activities (van Katwijk *et al.,* 2009), or by diversion of mud-rich or eutrophied water from an estuary at a system scale (e.g. Leston, Lillebø & Pardal, 2008) until restoration is complete and self-sustaining feedbacks restored. For example, transplant growth rates can be enhanced by suppressing the sediment-mobilising effect of bioturbators by applying a shell layer beneath seagrass transplants (Eklöf *et al.,* 2011; Suykerbuyk *et al.,* 2012). Due consideration needs to be taken of the scale- and density-dependent effects of seagrass meadows regarding water flow and sediment stabilisation (Lawson *et al.,* 2012). For instance, recent results from both seagrass and salt marsh restoration, indicate that facilitation may be harnessed by clustering plants or seeds (Bos & van Katwijk, 2007; Silliman *et al.,* 2015) although this approach is likely limited to systems with lower wave energy. Some actions might be useful in both conservation and restoration programs, for example prohibiting local activities such as anchoring or bait digging are important in order to establish and maintain strong self-sustaining seagrass feedbacks.

(4) Step 4: monitoring of feedback dynamics (e.g. feedback strength and effects on biotic and abiotic components)

Seagrass monitoring programs often only include state variables like biomass, density and cover. Ideally, however, a monitoring program should aim to include all system components in the feedback, i.e. the seagrass plants, associated biota and abiotic factors (such as sediments, light conditions, water-column characteristics) and the rates of the processes that drive the feedback. The analysis of system components provides an indication of how the feedback shapes the meadow according to established management goals. Process-based monitoring can be applied (e.g. in combination with associated research programs) for determining the effectiveness of actions taken to strengthen or maintain desirable feedbacks or weaken adverse feedbacks. For example, the strength of feedbacks promoting water clarity or sediment stability can be assessed by measuring and comparing water turbidity, sedimentation rates and flow velocity above seagrass beds and in neighbouring bare areas. In turn, critical densities and meadow extension to maintain
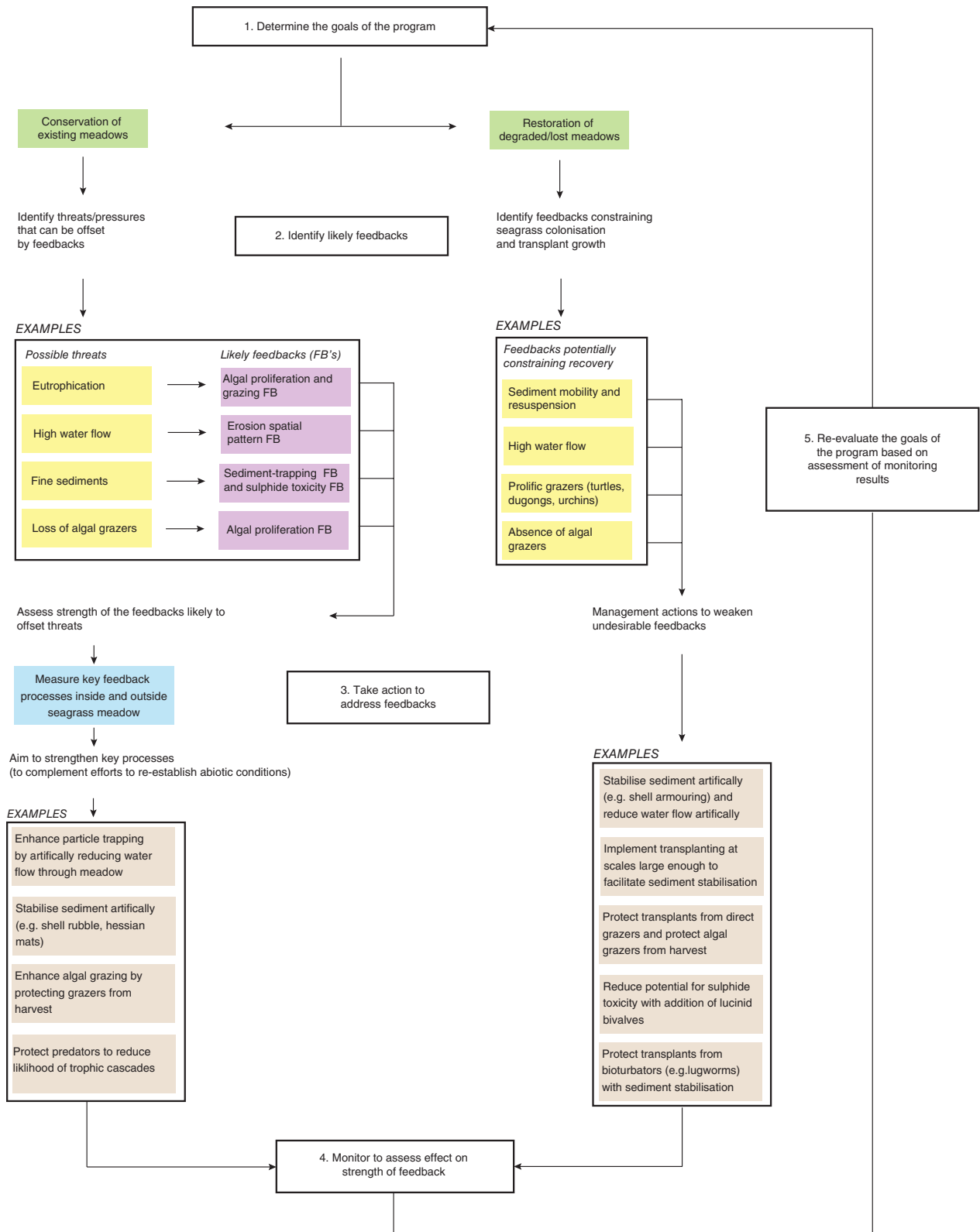
Fig. 6. Guidance for managers in identifying and prioritising feedbacks in seagrass ecosystems for conservation and restoration planning.

the feedbacks can be explored *via* relationships among seagrass state variables and turbidity, sedimentation rate and flow rate. Similarly, indicators for potential feedbacks in the non-seagrass state, like bioturbator densities (Suykerbuyk *et al.*, 2012), can be included.

In multi-species seagrass beds, species composition may serve as a supplementary indicator of the feedback strength related to sediment stability and hydrodynamics, as faster-growing species often have shallower roots and are less resistant to severe events like hurricanes (Cruz-Palacios & van Tussenbroek, 2005; van Tussenbroek *et al.,* 2014). Hence, disturbances or eutrophication may cause state shifts in species composition from slow-growing climax species to fast-growing pioneers (Fourqurean *et al.,* 2003; Cruz-Palacios & van Tussenbroek, 2005; Armitage, Frankovich & Fourqurean, 2011; van Tussenbroek *et al.,* 2014) which may, in turn, weaken the feedbacks related to sediment stability. Species composition as a supplementary indicator for feedback strength should, however, be examined in context with other potential drivers of the spatial structure of multi-species meadows (Ooi *et al.,* 2014).

Feedback mechanisms are context-specific, so management and monitoring programs that target feedbacks require detailed background knowledge. Monitoring programs can form the basis of ecosystem knowledge, which, in turn, can be used to fine-tune the monitoring as new questions arise (Carstensen *et al.,* 2011*a*). Most seagrass monitoring programs already include biotic as well as abiotic components but with the abiotic variables representing the conditions of the coastal area in general, and not measured at the scale of the seagrass meadow, which we recommend adding. A multitude of seagrass variables, ranging from state variables to process rates, are in use in existing seagrass monitoring programs with the most common indicators being shoot density, cover and depth limits (Marbà *et al.,* 2013). Particularly for slow-growing seagrass species or when beds are close to collapse, state variables may not be sufficiently sensitive to detect meadow decline over time and should, therefore, be supplemented with more-sensitive indicators, e.g. those related to process rates such as shoot recruitment and mortality rates, with higher capacity for early warning of state shifts (Marbà *et al.,* 2005, 2013; Soissons *et al.,* 2014). The timescales of response of a range of seagrass indicators to pressures have recently been reviewed, and the results may serve as guidance in the choice of sensitive indicators (e.g. McMahon, Collier & Lavery, 2013).

In seagrass landscapes, the spatial structure of seagrass patches has been related to changing abiotic conditions, suggesting potential use of self-organised spatial patterns as stress indicators in ecosystems (Fonseca *et al.,* 2008; Kendrick, Holmes & Van Niel, 2008; van der Heide *et al.,* 2010*a*). Despite still being exploratory, recent studies indicate that 'critical slowing down' may be useful as a method to assess ecosystem resilience (Carr *et al.,* 2012*b*; Soissons *et al.,* 2014; Dakos *et al.,* 2015). Critical slowing down of recovery rate has been shown to occur even when ecosystem state variables like per cent cover are still high, suggesting that traditional indicators of seagrass degradation, like decline of extent or cover may be inadequate to accurate forecasting of the onset of a shift in regime (Soissons *et al.,* 2014).

(5) Step 5: re-evaluate the goals of the program

Accounting for feedbacks adds a level of complexity to conservation and restoration programs, because it requires ecosystem-scale analysis. Because seagrass meadows are complex adaptive systems, this degree of system understanding is essential to increase both the success of management programs and the understanding of seagrass ecosystem dynamics. If management actions have been ineffective in reducing adverse feedbacks, these actions need to be either changed or improved. It is also possible that the site may not yet be suitable for restoration. In this case it is necessary to reduce stress levels to an extent to which seagrass restoration or recovery is possible.

VI. CONCLUSIONS

(1) Although it currently remains unclear whether feedbacks are generally strong enough to cause true alternative stable states, numerous studies have demonstrated that these mechanisms play a major role in the structure, functioning and fate of seagrass ecosystems. Appreciation of how feedbacks stabilise and destabilise seagrass meadows may therefore increase the success of seagrass conservation and restoration efforts.

(2) We provide evidence from throughout the seagrass literature on how current understanding of feedbacks can be applied to develop management strategies to increase the resilience of seagrass ecosystems to environmental stressors.

(3) Feedback mechanisms can act with varying intensity over gradients of environmental and ecological stress and are species and environment specific. Feedbacks operate at an ecosystem level and involve multiple trophic-level interactions between the seagrass meadow, associated organisms and the physical environment.

(4) Although a myriad of feedbacks have now been identified in seagrass ecosystems, interactions among feedbacks have been largely overlooked to date due to difficulties in analysis and detection. Modelling the interactions among two distinct above- and belowground feedbacks in seagrass ecosystems has shown that interacting feedbacks are likely to be important for ecosystem resilience and represents a significant avenue for the future understanding of feedback dynamics in ecosystems.

VII. ACKNOWLEDGEMENTS

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. The feedback mechanisms known to occur in seagrass ecosystems (also summarised in Table 1).

Appendix S2. Conceptual model of interacting feedbacks.