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Review

A framework for the resilience of seagrass ecosystems

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ABSTRACT

Seagrass ecosystems represent a global marine resource that is declining across its range. To halt degradation and promote recovery over large scales, management requires a radical change in emphasis and application that seeks to enhance seagrass ecosystem resilience. In this review we examine how the resilience of seagrass ecosystems is becoming compromised by a range of local to global stressors, resulting in ecological regime shifts that undermine the long-term viability of these productive ecosystems. To examine regime shifts and the management actions that can influence this phenomenon we present a conceptual model of resilience in seagrass ecosystems. The model is founded on a series of features and modifiers that act as interacting influences upon seagrass ecosystem resilience. Improved understanding and appreciation of the factors and modifiers that govern resilience in seagrass ecosystems can be utilised to support much needed evidence based management of a vital natural resource.

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1. Introduction

Seagrass meadows are critically important for the goods and services they provide maritime nations globally (Orth et al., 2006). This includes significant support for global fisheries (Gillanders, 2006; Lilley and Unsworth, 2014), the storage of sedimentary carbon (Fourqurean et al., 2012), and the filtration and cycling of nutrients (Hemminga and Duarte, 2000). In some parts of the world (e.g., SE Asia) seagrass meadows supply the daily protein and support a way of life of millions of people (Cullen-Unsworth et al., 2014; Unsworth et al., 2014). Despite their high value, these ecosystems continue to decline at alarming rates (Waycott et al., 2009) with localised management successes (e.g., improvements in water quality, and localised protection measures) failing to reverse regional and global scale declines (Waycott et al., 2009). If global degradation of seagrass meadows is to be halted and patterns of recovery observed over large scales, management of these systems needs to undergo a radical change in emphasis and application. A means of making such radical change is to undertake action that seeks to enhance ecosystem resilience (Orth et al., 2006; Waycott et al., 2009). Environmental managers across the globe are embracing the concept of resilience as a tool in ecosystem management for natural systems, e.g., managing herbivore populations on coral reefs (Graham et al., 2013), while progress within seagrass ecosystems however remains lagging.

Ecological resilience is “the capacity of an ecosystem to absorb repeated disturbances or shocks and adapt to change without fundamentally switching to an alternative stable state” (Holling, 1973). Resilience relates to how an ecosystem resists stressors and how it recovers from loss or degradation (resilience = resistance and recovery). In previous studies, resilience in seagrass ecosystems has been investigated at the level of the plant and its interactions with the abiotic environment, and with respect to the cascading impacts of grazer communities upon this resilience (Alsterberg et al., 2013; Carr et al., 2012; Duarte, 1995; Duffy et al., 2003; Eklof et al., 2012; Garrido et al., 2013; Han et al., 2012). Although we have extensive experimental evidence of these processes they have not been conceptualised into a framework demonstrating what resilience is within a seagrass ecosystem and how it operates.

Here we propose a conceptual model of resilience in seagrass ecosystems, arguing why such a model is required, and reviewing evidence in support of the features and modifiers of seagrass resilience. This is placed in the context of the value of seagrass ecosystems to humanity and how seagrass ecosystems can potentially undergo an ecological regime shift leading to loss of habitat. We conclude by discussing how a greater level of understanding and appreciation for the factors that control resilience in seagrass ecosystems can be utilised to support much needed evidence based management of this global resource.

2. Global seagrass loss

The decline or sometimes complete loss of seagrass meadows can result in severe economic losses to society. Regardless, over the last century, seagrasses have become increasingly affected by human activities, illustrated by severe declines in habitat or species loss that are often characterised by sudden change (e.g., total loss of a meadow) (Orth et al., 2006; Waycott et al., 2009). This phenomenon supports the theory of critical ecosystem tipping points (Horan et al., 2011), beyond which habitat degradation is inevitable. As a result of sudden changes, ecosystems sometimes undergo an ecological regime shift described as “a sudden shift in ecosystem status caused by passing a threshold where core ecosystem functions, structures and processes are fundamentally change” (Andersen et al., 2009; Lees et al., 2006).

Loss, change or species disappearances within seagrass meadows are usually correlated with decreases in light availability, eutrophication, increases in sedimentation, or direct physical disturbance (Erftemeijer and Lewis, 2006; Waycott et al., 2009). Other stressors such as the presence of invasive species and disease can also lead to

habitat degradation (Williams, 2007). Other, larger cascading impacts, related to the alteration of the food web may also be drivers of loss but these have not received as much attention as the abiotic processes.

Failure of seagrass to recover, even after the primary stressor has been removed that is possibly the result of a regime shift to one of high turbidity, increased suspended sediment and anoxic sediments (Viaroli et al., 2008), conditions considered antagonistic to seagrass survival and recovery (Carr et al., 2012; McGlathery et al., 2013). In multi-species meadows multiple alternative regimes are possible due to climax communities becoming replaced by ruderal species (Johnson et al., 2003). For example, after initial loss of *Thalassia hemprichii*, these communities can become dominated by smaller colonising flora such as *Halophila ovalis*. In the Mediterranean, *Posidonia oceanica* communities after loss have been found to become dominated by *Cymodocea nodosa* (Delgado et al., 1997). Should degradation continue a system can become dominated by a changed community such as anoxic mud containing no seagrass (Fig. 1). Such changes have been observed leading to the proposal that regime shifts occur due to positive feedback mechanisms between seagrasses and their abiotic environment (Carr et al., 2010; van der Heide et al., 2007; Walker et al., 2006).

Multiple large-scale stressors in the marine environment such as declining water quality, increasing storm frequency and intensity, exacerbate the slow incremental degradation of seagrass meadows caused by local or regional scale stressors. Smaller scale stressors that influence meadow or patch scale processes include local physical disturbance and altered food-webs. All of these stressors work to reduce the capacity of seagrass meadows to be resilient in the face of other global-scale environmental changes in particular increasing sea surface temperature (SST) and sea level rise (Saunders et al., 2013). Further information on how these stressors interact at the ecosystem and landscape scale to influence ecosystem resilience is needed to better understand the key pressure points so that management can be appropriately targeted.

3. Seagrass ecosystem drivers

Natural ecosystems respond to drivers over variable timescales. Responses are separated into ‘fast’, ‘threshold like’ responses to stressors, and ‘slow’ linear responses to slowly developing pressures such as fishing, elevated nutrients or rising global temperatures (Hughes et al., 2003). Non-linearity can make the response of systems difficult to predict (Koch et al., 2009), particularly in the presence of multiple drivers of change. Slow, ‘chronic drivers’ may occur simultaneously, and may be highly interactive with each other, causing cellular or physiological responses that are not readily quantified (Hughes et al., 2010). In contrast, fast drivers (e.g., large storm events or periods of extreme temperature) are episodic disturbances or shocks that quickly push the system away from its equilibrium state (Hughes et al., 2010).

Seagrass meadows are commonly subjected to stress from fast ecosystem drivers and rapidly elicit responses, but change is manifested differently between species (Erftemeijer and Lewis, 2006). When chronic levels of stress (slow drivers of change) are low (below a threshold) a seagrass ecosystem may have features that provide it with the capacity to recover from an acute, fast-acting disturbance (sub-lethal or lethal) (Fig. 2). For example, a seagrass meadow in Australia underwent a long-term cycle of ‘boom and bust’ resulting in complete loss driven by high temperatures and limited rainfall. The seagrass recovered due to low levels of chronic stress and the presence of a large seed bank (a recovery feature of a resilient system) (Rasheed and Unsworth, 2011). The seagrass community showed no susceptibility to undergo a long-term shift to an alternative regime. In contrast, many meadows globally have been subjected to persistent chronic levels of stress, leaving them in a weakened state (with limited features of resilience) and unable to recover from episodic disturbance. For example, chronic eutrophication has been found to increase algal and epiphytic cover within a *Zostera marina* meadow, reducing light availability and impeding its capacity to produce a viable seed bank, leaving the

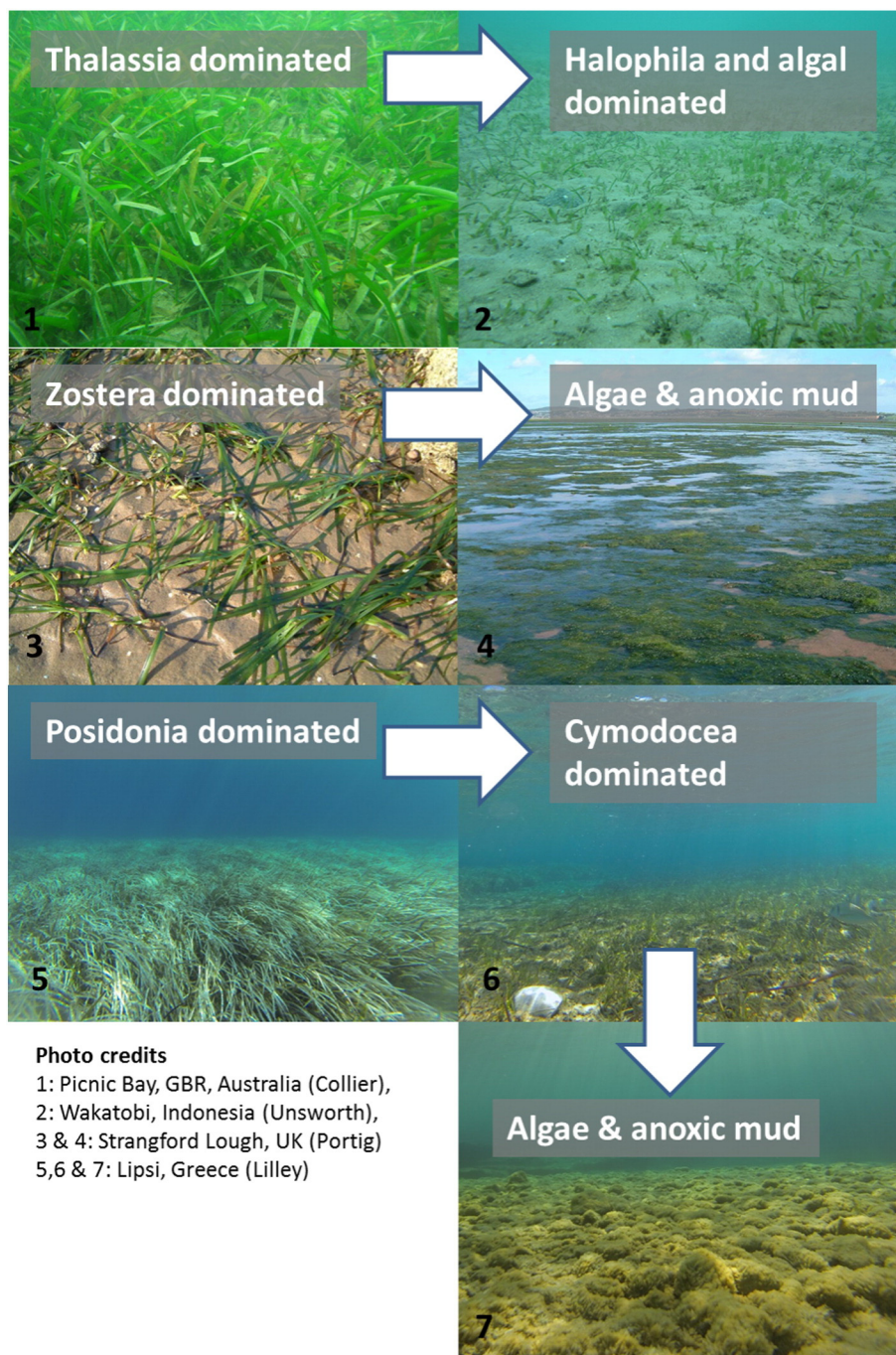


Fig. 1. Observed regime shifts in tropical and temperate seagrass meadows over one and two steps. The failure of seagrass to recover, even after the primary stressor has been removed is possibly the result of a regime shift to conditions considered antagonistic to seagrass survival and recovery (one step). In multi-species meadows, multiple alternative regimes are possible (two steps) due to climax communities becoming replaced by ruderal species before becoming devoid of seagrass.

meadow vulnerable to environmental shocks (van Katwijk et al., 2010b). When subjected to an episodic disturbance the seagrass meadow may then fail to recover after loss.

For seagrass meadows to remain resilient to episodic 'fast drivers' of ecosystem change, they must have the necessary energetics to recover and/or the reproductive capacity to regenerate (Collier and Waycott, 2009; Erftemeijer and Lewis, 2006; Jarvis et al., 2014). In response to an episodic driver (e.g., a storm event) the immediate impact could be the mortality of individuals due to physical damage. In this case resilience is therefore likely to depend on features of 'recovery' (e.g., the presence of a seed bank). An alternate scenario is one where the fast driver (e.g., a storm event) does not cause mortality or physical harm

but instead results in a sustained period of turbidity. In this scenario the seagrass plants will need to resist degradation and so will be dependent upon features of 'resistance'. The individual plant may possess traits such as the presence of carbohydrate storage reserves that provide a means of 'resistance' to deal with a period of negative carbon balance (e.g., induced by limited light availability). These individual traits, when common within a community, confer a level of resilience sufficient to prevent ecosystem change (Bergmann et al., 2010; Ehlers et al., 2008; Reusch and Hughes, 2006).

The cumulative effects of multiple stressors, whether of anthropogenic or natural origin, are likely to impact coastal meadows due simply to their geographical positioning at the interface of multiple

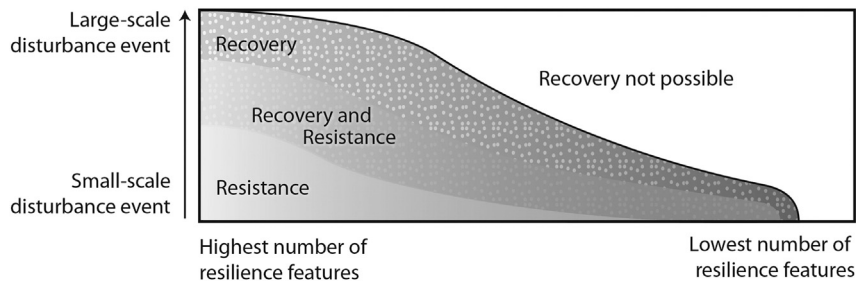


Fig. 2. Resilience is comprised of both resistance (grey shade) and recovery (spotted fill) processes. With the highest number of resilience features (left of plot), seagrass meadows can resist and/or recover from large-scale disturbance events. Recovery is more critical for resilience to very large events, when for example, seed banks may enable a meadow that has been completely removed to re-grow. As the number of resilience features declines (moving right), the scale of the event from which the meadows can resist or recover from, is reduced.

human–environmental interactions (Blake and Duffy, 2010; Kenworthy et al., 2006). For example, persistent poor water quality, low light-limited photosynthetic carbon fixation (via photosynthesis) and low energetic surpluses (low production/respiration), commonly found in coastal environments reduce the capacity of a plant to store energy reserves, thus limiting its ability to resist or recover from further stress (Eklof et al., 2009). These factors can act synergistically creating an impact that is greater than the sum of individual stressors, resulting in reduced resilience systems (Brown et al., 2014) (see Fig. 3).

4. Seagrass ecosystem resilience

Integrating concepts of ecosystem resilience into conservation practice necessitates an understanding of what the key features of a resilient ecosystem are, the modifiers of that resilience, and the means to maintain resilience. The features and modifiers can be conceptualised as a series of interacting influences upon the resilience of seagrass ecosystems (Fig. 4) and can be grouped as 1) biological features of resilient seagrass; 2) the biophysical environment; and 3) biological features of a resilient supporting ecosystem.

4.1. Biological features of resilient seagrass

The ‘insurance hypothesis’ posits that more biodiverse ecosystems are more likely to contain individuals, taxa or habitats capable of withstanding or surviving a given disturbance and as such they can compensate for those more susceptible (Tilman, 1996; Yachi and Loreau, 1999). To promote seagrass resilience, all three levels of biological diversity (genetic, species and ecosystem) are important (Campbell et al., 2006; Christianen et al., 2011; Reusch et al., 2005). Therefore, here, we propose that genetic diversity, species (plant) diversity, continuous habitat, and species biological traits (energy reserves, growth strategy and seed banks) are the four dominant biological features that contribute to the

resilience of the seagrass plants themselves. The following discusses the evidence for the role each of these as features of resilience.

4.1.1. Genetic diversity

Defining the biological traits and consequently the resilience of a seagrass meadow by its species richness alone is not always appropriate. Phenotypic variation (the expression of genetic traits) can create diversity in morphometric and resilience traits and can be as large within species as between species (Bangert et al., 2005). In addition, genetic diversity can produce population- and community-level ecological effects similar to those of species diversity (Hughes and Stachowicz, 2011; Reynolds et al., 2012b). Genotypic diversity can replace the role of species diversity in species-poor coastal ecosystems and studies indicate that this may help buffer against extreme climatic events by providing enhanced physiological resistance (Reusch et al., 2005). The response of individual species to different environmental conditions can be observed through its morphological plasticity (e.g., leaf width and length) and physiological adaptability (e.g., range of tolerance to key abiotic features such as salinity or light availability). The dominant seagrass traits for survival follow a broad model that aligns with groups of seagrass genera sharing ranges of these traits (Kilminster et al., in press).

Not all seagrass genera have high plasticity (indicated by morphological plasticity) with some genera (e.g., *Enhalus*) having relatively low levels of plasticity while others such as *Halophila* exhibit extreme plasticity (Carruthers et al., 2007; Collier and Waycott, 2014; Maxwell et al., 2014; Waycott et al., 2002). Resistance to disturbance can be inferred through detection of long-lived individuals and clonality. Recognition that clonality occurs in a diverse range of seagrass species and situations (Alberto et al., 2001; Arnaud-Haond et al., 2012; Reusch et al., 1999; Waycott et al., 2006; Waycott et al., 1996) has been important for inferring the persistence of plants over very long time scales. At the same time, most seagrasses produce seeds or seedlings regularly

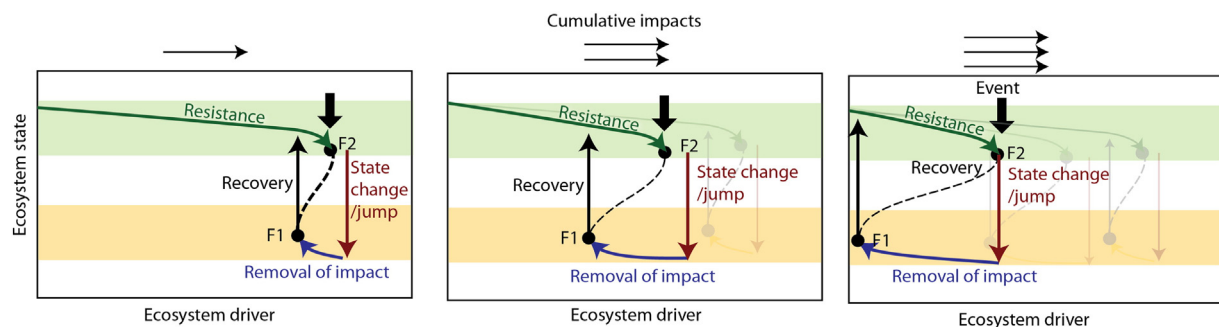


Fig. 3. Worsening environmental conditions (often of a cumulative nature) or a large disturbance event can force seagrass ecosystems to undergo a regime shift. This shift could be analogous to a change in community from one that is a climax community (flora and fauna) existing in a state of meadow maintenance, to one that is a community in a colonizing state dominated by disturbance and species exhibiting colonizing traits. Once the physical disturbance has passed, a resilient meadow (left panel) will return on a trajectory of recovery without significant intervention. A meadow with increasing numbers of cumulative impacts (becoming non-resilient) will more easily undergo a regime shift at lower environmental pressure as it doesn't have the capacity to resist. Furthermore, a non-resilient meadow requires a much greater push back to enable recovery to original community status.

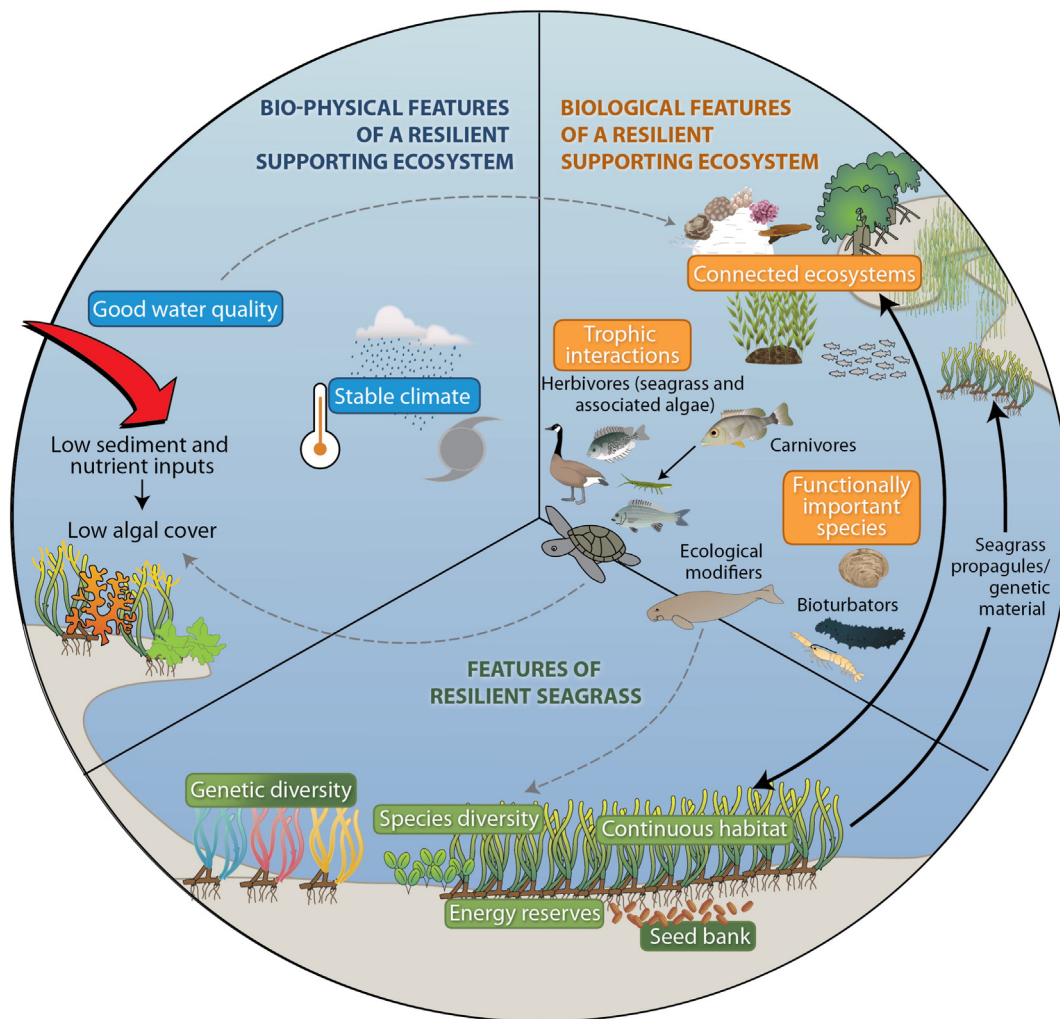


Fig. 4. The resilience of seagrass ecosystems is dependent on multi-faceted aspects of the seagrass meadow itself as well as features of the surrounding biological and bio-physical environment. Specifically, resilient seagrass ecosystems may have some of the following features: high genetic diversity; high species diversity; continuous (not fragmented) habitat; energy reserves; and a robust seed bank. The relative importance of these resilience features depends largely on the floral species. These characteristics of a resilient seagrass are supported by balanced grazing pressure from herbivores (mega-herbivores, fish and epiphyte grazers) and carnivores. Supply of grazers is frequently coupled with connectivity to adjacent habitat (seagrass and non-seagrass, such as salt marsh, coral reef, algal reef and/or mangroves). Connectivity to other seagrass meadows supplies of propagules (plants and seeds) and larvae, and allows for the sharing of genetic material resulting in greater resilience due to more diverse and therefore adaptable populations. Critical bio-physical features of a resilience seagrass ecosystem include moderate temperatures (lacking temperature anomalies or extremes) and good water quality (low turbidity and low-moderate nutrients). Water quality also affects the abundance of other primary producers such as macroalgae and epiphytes, which can reduce the resilience of seagrass at high abundances.

(Kendrick et al., 2012). The combination of clonality and ongoing reproduction most likely represents a strategy of ‘bet-hedging’ (Philippi and Seger, 1989), or waiting for windows of opportunity (Eriksson and Fröberg, 1996) and is common in recruitment limited systems enabling long term resilience in the face of environmental variability. Assessment of genetic variability enables determination of the scale of reliance on clonality through the measurement of genotypic identity (Arnaud-Haond and Belkhir, 2007). However, these features only infer resistance to stressors and more direct evidence through experimental testing of species’ varying ability to exhibit plasticity to perturbations is needed.

In a manipulative field experiment, increasing the genotypic diversity of *Z. marina* (that persists mostly mono-specifically) enhanced meadow recovery rate from stress. The higher diversity plots had higher biomass production, plant density, and faunal abundance, despite near-lethal water temperatures due to extreme warming across Europe (Reusch et al., 2005). Other experiments that have manipulated the genotypic diversity of *Z. marina* have found that genotypic diversity enhanced resistance to disturbance, but only at the highest level of disturbance. The high genotypic diversity plots also had greater resistance (loss of fewer shoots) to disturbance induced by increases in macroalgae (Hughes and Stachowicz, 2011).

Other experimental studies on *Z. marina* have found a strong negative effect of warming and a positive effect of genotypic diversity on shoot density (Ehlers et al., 2008). These experiments investigating the response of seagrass of variable genetic diversity to warming suggest that although seagrass meadows are negatively affected by increasing temperatures, genotypic diversity may provide critical response diversity for maintaining seagrass ecosystem functioning, and for adaptation to environmental change (Ehlers et al., 2008). Genetic diversity of *Z. marina* enhances restoration success, appearing to act through increased productivity (Reynolds et al., 2012a; Reynolds et al., 2012b). A major limitation in our perception of how genetic diversity strengthens the resistance and recovery of seagrass systems is that our understanding of resilience, through experimental approaches, has predominantly come from work conducted only on *Z. marina*.

4.1.2. Species diversity (floral) and biological traits

Biological traits exhibited by organisms affect their behavioural, physical and physiological responses to stimuli such as environmental change (Lavorel et al., 2007). In terms of both resistance and recovery of a seagrass meadow, the greater the variability of traits present, and their plasticity, the more likely the system is to survive periods of stress.

The highly variable and species-specific response to elevated temperatures for species inhabiting a single multi-specific meadow illustrates the variety of between species biological traits present (Campbell et al., 2006) and how such diversity might contribute to greater meadow resistance capacity (Kilminster et al., in press).

Seagrasses species exhibit a wide array of morphological and life history traits that are key to how they adapt to variable environments and either resist or recover from stress. The life history traits of all 13 seagrass genera have been scaled (Walker et al., 1999) from those that are ephemeral and rely on seed banks (sexual reproduction) for recovery, such as *Halophila*, to *Posidonia* that is fully persistent and forms a climax community employing traits that confer resistance, such as energy reserves (Carruthers et al., 2007; Kendrick et al., 2012) (see Table 1). Reduced dependence on a specific trait doesn't necessarily make a plant less resilient but reflects the greater reliance on *different* life history traits. The relative reliance on resistance traits such as larger energy stores versus recovery traits such as a persistent seed bank or long dispersal distances represent well recognised functional forms for seagrasses (Walker et al., 1999).

Slow growing seagrasses such as species of *Thalassia* or *Posidonia* that form a climax community typically develop large carbohydrate stores which they use to resist short or medium term disturbances (Marba et al., 1996). Under optimal conditions, these species build stores of non-structural carbohydrate within their rhizomes which can be mobilised to sustain the plant temporarily during periods of stress, particularly stress that reduces net photosynthesis (Alcoverro et al., 1999; Collier et al., 2009; Erftemeijer and Lewis, 2006). Carbohydrate stores vary as a function of space and time and reflect the recent energetic balance of the plant. Disturbances that result in the depletion of

carbohydrate reserves make seagrass meadows more vulnerable to additional stress (Eklof et al., 2009).

Smaller fast growing species such as *Halophila* spp., and to a lesser degree *Halodule* spp., do not maintain such large carbohydrate reserves, and therefore employ additional mechanisms to confer resilience upon the community (Erftemeijer and Lewis, 2006) such as the maintenance of a viable 'seed bank' (see Table 1). Faster growing species commonly produce seeds that remain dormant in the sediment for extended periods (months to years), producing a seed bank from which recovery can occur (Jarvis et al., 2014). But these seed banks are also highly variable through space and time (Cabaco and Santos, 2012). Longevity of seeds also varies between species (Rasheed, 2004), with some species germinating before release and others remaining viable for years once released (Kendrick et al., 2012). After major seagrass 'die-off' events, recovery is assisted by recolonization from seed banks present within the sediment (Campbell and McKenzie, 2004). The seed bank contributes to the 'insurance policy' to cope with future episodic stress events conferring some level of resilience upon the meadow (Reynolds et al., 2013). But as with other components of a seagrass meadow the seed bank can be susceptible to anthropogenic impacts such as eutrophication (van Katwijk et al., 2010a), consequently reducing capacity for resilience.

Following disturbance in a multi-species meadow, seed bank-induced recovery by r-strategists (such as *Halophila* spp. and *Halodule* spp.) can stabilise substrates and form the basis for later recolonisation by K-strategists, such as *Thalassia* (Birch and Birch, 1984). However, drivers of seed production and seed bank longevity are not well known for many species. The continuum of the adaptive strategies that exist across seagrass genera (Kilminster et al., in press) represents

Table 1
Variability in functional traits observed between three seagrass species of different life history and genera.

		Reducing size and faster turnover →		
		<i>Posidonia oceanica</i>	<i>Zostera marina</i>	<i>Halophila decipiens</i>
<i>Species descriptors</i>				
Biomass	Total biomass (BGr + AGr gDW m ⁻²)	2111.7 ¹	448.1 ¹	140.5 ¹
	BGr/AGr biomass	3.2 ¹	0.5 ¹	1.2 ¹
Growth	Leaf growth (cm shoot ⁻¹ day ⁻¹)	0.8 ²	3.2 ²	n/a
	Rhizome extension (cm yr ⁻¹)	4.2 ²	40.9 ²	215 ²
	Turnover rates (yr ⁻¹)	1.87 ²	11.17 ²	32.36 ²
<i>Features of resilience</i>				
Reproduction	Flowering intensity (% of shoots)	8 (0–20) ^{3,4,5}	24 (15–33) ^{6,7,8}	4 (0–198.8) ⁹
	Seeds per inflorescence	1 ⁴	6 (2–11) ^{8,10}	32 (0–58) ^{9,11,12}
	Seed density (1000 m ⁻² yr ⁻¹)	0.007 (0–0.014) ^{4,5,13}	35 (6–100) ^{8,10,14}	64 (0–176) ¹¹
Reserves	Carbohydrate concentration (starch + soluble, %DW)	14.0 (4.4–25.5) ^{15,16,17}	17.4 (7.2–27.9) ¹⁸	9.3 (4.3–12.6) ¹⁹
Genetic diversity	Observed heterozygosity H ₀	0.44 (0.43–0.45) ²⁰	0.53 (0.43–0.8) ^{20,21}	No data

¹ Duarte and Chiscano (1999).

² Duarte (1991).

³ Diaz-Almela et al. (2006)

⁴ Balestri and Cinelli (2003).

⁵ Balestri and Vallerini (2003).

⁶ Ochieng and Erftemeijer (1999)

⁷ Silberhorn et al. (1983).

⁸ Jarvis (2014).

⁹ Hammerstrom et al. (2006).

¹⁰ Meling-Lopez and Ibarra-Obando (1999).

¹¹ Kuo and Kirkman (1995).

¹² McMillan and Soong (1989).

¹³ Buia and Mazzella (1991).

¹⁴ Orth et al. (2006).

¹⁵ Ruiz and Romero (2001).

¹⁶ Alcoverro et al. (2001).

¹⁷ Pirc (1989).

¹⁸ Burke (1996).

¹⁹ McDermid et al. (2007).

²⁰ Kendrick et al. (2012).

²¹ Reynolds et al. (2012a).

a significant component of how species composition in seagrass communities confer resilience.

Our perception of seagrass meadow loss, and its subsequent recovery, reflects the life history traits of the species' involved. The absence of a visible meadow on the seabed does not necessarily mean that the meadow has been lost indefinitely and shoot recovery can be quite rapid (Macreadie et al., 2014). The ability of meadows to recover is largely species specific and dependent upon the persistence of the rhizome or the availability of sexual or asexual propagules (Jarvis et al., 2014; Macreadie et al., 2014; Rasheed, 2004). Within a tropical *Halophila* meadow, after a moderate impact there may be no shoots or rhizomes present, however an abundant seed bank will likely remain, conferring a means of recovery (Erftemeijer and Lewis, 2006). The impacted *Halophila* meadow contrasts with a *Thalassia* or *Posidonia* meadow whose shoots have mostly disappeared after moderate impact but whose rhizomes still remain with some live shoots. Recovery from live rhizomes can be enhanced by a higher density of live shoots at the start of recovery (Collier et al., 2009). Both meadows are still present but with reduced visibility, and both are vulnerable because their capacity to recover is reduced. Critically, and dependent upon previous levels of stress (ability to store carbohydrates or produce seeds), both have a source of resilience which may allow them to recover.

4.1.3. Continuous (non-fragmented) habitat

Seagrass meadows commonly comprise a spatial mosaic of un-vegetated and vegetated areas (Bell et al., 1999). With greater levels of disturbance (natural or anthropogenic) the un-vegetated areas become larger and more frequent, resulting in meadow fragmentation (Short and Wyllie-Echeverria, 1996; Tewfik et al., 2007). With increased fragmentation the capacity for the meadow to recover from disturbance may decrease for two reasons. Firstly, meadow recovery from small scale disturbance (e.g., anchor damage) is often through rhizome elongation to the damaged area (Rasheed, 2004). With greater fragmentation the likelihood of a rhizome being sufficiently proximate to the damaged area to facilitate recovery is reduced. Secondly a fragmented meadow may have reduced sexual reproductive output (Cabaco and Santos, 2012; Vermaat et al., 2004).

Once fragmented, a meadow loses stability further reducing resilience. This is because mortality risk is patch size-dependent and patch losses are often confined to smaller patches below a certain threshold size (Duarte et al., 2006). Studies have shown that increased levels of fragmentation result in decreased capacity to resist the impacts of storms (Fonseca and Bell, 1998). A small isolated patch of seagrass if subjected to stress may then have a reduced recovery capacity if it is dependent upon self-recruitment and regeneration.

4.2. Biological features of a resilient supporting ecosystem

Typically seagrass meadows are monitored and assessed at the habitat (plant) level and sampling is designed to examine meadow temporal and spatial population changes. However, understanding and assessing the resilience of a seagrass meadow requires more than just habitat level information, it requires an understanding of how its associated ecosystem helps confer resilience upon it. Here we separate ecosystem level features that confer resilience into three groupings: 1) trophic interactions, 2) connected ecosystems, and 3) functionally important species.

4.2.1. Trophic interactions

Both 'top-down' and 'bottom-up' factors can act in concert to determine the structure and function of coastal ecosystems (Lotze et al., 2006). By feeding on lower order predators and consumers, apex predators can alter the rates of ecosystem primary productivity and the structure of benthic communities (top-down processes). Furthermore, growth and productivity of benthic systems such as seagrass can drive

the dynamics of faunal communities (Jackson et al., 2006). The relative strength of these processes remains debatable but it is clear that both are important in determining the structure of seagrass systems and therefore their resilience.

Marine ecosystems are increasingly characterised by the loss of top predators, with many also devoid of lower order consumers. This creates an altered food web with potentially increased abundance of specific groups such as herbivores or smaller predators, and with potential cascading effects that result in seagrass overgrazing or insufficient control of epiphytes (Heck and Valentine, 2007). Top-down impacts can also be synergistic with bottom up drivers such as poor water quality. As epiphyte biomass increases, the mesograzing community (that consume epiphytic algae) becomes increasingly important for controlling growth, reducing the potential for algae to suffocate or limit light availability to the seagrass (Best and Stachowicz, 2012; Whalen et al., 2012). When trophic cascades result in decimation of the mesograzing community, the seagrass meadow may lose some of its capacity to resist the impact of poor water quality (through the build-up of epiphytic growth), and hence its resilience is reduced (Baden et al., 2012; Hughes et al., 2013). The presence and diversity of a mesograzing community are important for controlling epiphytic algae (Duffy, 2002). Global experimental studies on *Z. marina* have demonstrated that diversity of the invertebrate mesograzing community is comparably important to global change stressors in the top-down control of seagrass ecosystems (Duffy et al., 2015).

There is increasing appreciation for the role of herbivory (sea urchins, parrotfish, sea turtles, waterfowl, dugongs, and manatees) in conferring resilience upon seagrass ecosystems (Christianen et al., 2011). This herbivory may decrease accumulation of organic matter in sediments, reducing sediment hypoxia and stimulating biodiversity (Valentine and Duffy, 2006). It may also increase the turnover of leaves, lessening the potential for algal overgrowth and attack by disease vectors such as slime moulds (Valentine and Duffy, 2006). This consequently increases the resistance of the system to stressors. In tropical seagrass systems the negative effects of eutrophication have been shown to be alleviated by sea turtle grazing (Christianen et al., 2011). Studies have also shown that herbivory (i.e., dugong grazing) can alter seagrass species assemblages, maintaining a habitat of colonising seagrass species (Preen, 1995) and therefore indirectly altering the typical community type that occurs in the system and leading to a different resistance and recovery profile.

4.2.2. Connected ecosystems

The movement of organisms and biological and chemical material between habitats facilitates habitat connectivity leading to; the persistence of populations, increasing meadow scale productivity and improved recovery from disturbance. Seagrass meadows are connected with adjacent mangroves and coral reefs in the tropics, and salt marsh, oyster reefs and sandy shores in temperate regions. The linkages between the different ecosystems are the result of factors such as fish and invertebrate nursery use, carbon flow and foraging (Heck et al., 2008; Nagelkerken, 2009; Olds et al., 2014). The breakdown of these links will negatively influence the resilience of seagrass ecosystems.

4.2.3. Physical processes

Connections to, and protection provided by, nearby habitats can alter the biophysical environment, modifying the resilience of a marine habitat (van de Koppel et al., 2015). Protecting the resilience of seagrass meadows may necessitate the conservation of adjacent habitats and the linkages between them (van de Koppel et al., 2015). In the tropics, coral reefs buffer ocean currents and waves creating a suitable environment for seagrasses, while mangroves stabilise sediments, slow water movements and trap heavy metals and nutrient rich land run-off, thus improving the water quality for seagrass communities (Saunders et al., 2014). As a result of these interactions, degradation of a connected coral reef or mangrove habitat can have adverse effects on the resilience

of a seagrass system (and of course vice versa). For example degraded coral reef systems dissipate less wave energy resulting in higher wave energy within lagoon seagrass meadows (Saunders et al., 2014). In temperate seagrass meadows degradation and loss of salt marsh have been demonstrated to result in increased nutrient loading into adjacent seagrass meadows (Valiela and Cole, 2002).

4.2.4. Reproduction

Maintenance of genetic diversity enables seagrass meadows to have greater resilience and as such this requires a source of new genetic material, either as propagules, fragments or as pollen (Kendrick et al., 2012). Pollen and seeds both drift within the water column, within and between meadows. Although pollination of seagrass flowers has previously been thought to be hydrophilous, zoophilous pollination by macro invertebrates is also possible (van Tussenbroek et al., 2012). There is also growing evidence of a faunal contribution to seed dispersal (Sumoski and Orth, 2012). Understanding the supply of reproductive material is another key element to determining the potential resistance and recovery capacity of a meadow. Supply of seed material is highly variable between species with some seeds recorded to travel up to 400 km, and others only a few metres (Kendrick et al., 2012). Pollen has less capacity to travel long distances as it is only viable for short periods of time and lacks the necessary architecture for long distance travel (Kendrick et al., 2012). Maintenance of connectivity is not only a function of dispersal distance but critically also of local circulation that, if undesirable, can render an otherwise healthy meadow to be recruitment limited. In seagrass systems detecting connectivity of plants among populations is difficult and so measurement of connectivity is typically done using genetic markers (Arnaud-Haond et al., 2007; Reynolds et al., 2013).

4.2.5. Faunal migrations

The trophic structure and species assemblages of motile fauna in seagrass are influenced by the configuration of adjacent habitats (Irlandi and Crawford, 1997; Nagelkerken, 2009). Given that the density of functional groups can change with habitat configuration (Nagelkerken, 2009), this indicates potentially variable levels of resilience driven by their location relative to other habitats.

Landscape variability (within and between meadows) also affects the functional role (in terms of food availability and/or predation risk) of a meadow for supporting fish (Bostrom et al., 2011). Whether such assemblages that differ in their functional trophic role are of importance to resilience of the meadow requires further research attention.

4.2.6. Additional functionally important species and groups

Lucinid bivalves are globally abundant in seagrass meadows (Reynolds et al., 2007; van der Heide et al., 2012). The symbiosis that these bivalves have with sulphide oxidizer bacteria is key to reducing toxic sulphide levels in the sediment (Reynolds et al., 2007; van der Heide et al., 2012). Consequently the presence of these bivalves enhances seagrass productivity, enabling a healthier and more resilient seagrass community to exist.

Other faunal groups (e.g., holothurians, goatfish and Callianassid shrimp) within seagrass meadows potentially also exert a major functional effect on the processes of recovery and resistance. Many such species are exploited as food items around the world (Unsworth and Cullen, 2010), particularly the abundant bioturbating organisms. The limited evidence available suggests that bioturbaters can enhance sediment oxygenation and the remobilising and cycling of nutrients and are important for burial of litter and seeds (Blackburn and Orth, 2013; Kneer et al., 2013). Seagrass systems have been found to suffer in the absence of holothurians due to their role in remobilising nutrients (Wolkenhauer et al., 2010). In nutrient poor environments these functions may be critical for the maintenance and hence resilience of seagrass (Wolkenhauer et al., 2010). Goatfish (and possibly other fish species such as Snake eels and Wrasse) may also play a similar role in

seagrass meadows by disturbing surface sediments (Suchanek and Colin, 1986; Uiblein, 2007). The disturbance caused by Callianassid shrimp is so large that it alters seagrass species composition (Vonk et al., 2008), altering the life history traits present and therefore the resilience of the meadow. Bioturbation is an important process structuring seagrass ecosystems but mechanisms behind how this influences the resilience of the system remain unclear. This is a significant research gap within seagrass ecology.

4.3. Biophysical features of a resilient supporting ecosystem

An optimal biophysical environment enables a seagrass meadow to resist disturbance and recover from loss or degradation. While the biophysical environment of a pristine seagrass meadow is inherently variable, extreme conditions are mostly rare, and simultaneous chronic disturbances generally absent. Poor water quality, physical disturbance and climate change are examples of chronic and episodic stressors and can lead to conditions that reduce the resistance and recovery capacity of seagrass. However, there is evidence that exposure to some environmental stress may enable individuals or communities to adapt to the driver and improve their resistance (Maxwell et al., 2014).

4.3.1. Climate change and broad scale disturbance

Ocean acidification (OA), increasing temperature and sea level rise are increasingly impacting coastal ecosystems as the climate changes (Short and Neckles, 1999). OA is of lesser concern for seagrasses which can be limited by the availability of dissolved inorganic carbon (DIC), and will probably increase photosynthetic rates and biomass as the oceans become increasingly DIC enriched (Hall-Spencer et al., 2008; Ow et al., 2015; Russell et al., 2013). Even though this may not necessarily translate into higher growth rates (Campbell and Fourqurean, 2014; Ow et al., 2015; Palacios and Zimmerman, 2007), seagrasses will cope with OA and their uptake of DIC may partially buffer against OA for calcifiers at very localised scales (Unsworth et al., 2012). Negative impacts of climate change on seagrass will result from temperature changes (both chronic and short-term acute changes) and storm events (Short and Neckles, 1999). Climate related impacts and loss of seagrass have been recorded throughout the last few decades, linked to El Niño events and periods of extreme heating (Campbell et al., 2006; Rasheed and Unsworth, 2011). The direct effects of increased temperature depend on the individual species' thermal tolerances, including their optimum temperatures for photosynthesis, respiration and growth, and how these processes compete for carbon resources (Short and Neckles, 1999). Many seagrass species are already close to their upper temperature thresholds, with increasing temperatures likely to disturb their carbon balance (Collier et al., 2011; Massa et al., 2009), particularly in those also at the edge of their ecological niche (Marba and Duarte, 2010). Subtidal seagrass, particularly those near their depth limit, exist on a threshold where photosynthetic carbon gain is very closely balanced with respiratory carbon requirements (i.e., at their compensation irradiance) (McDonald, 2003). Compensation irradiance is increased at higher temperatures (Masini et al., 1995) and this could reduce colonisation depths (McDonald, 2003) while sea level is also rising; however, increased dissolved CO₂ may affect how plants tolerate reduced light levels at depth (Zimmerman et al., 1997).

Many of the temperature-related impacts in seagrass meadows have been in shallow or intertidal environments that are susceptible to extreme temperatures (Massa et al., 2009; Rasheed and Unsworth, 2011). Seagrass 'burning' occurs when temperatures, exacerbated by low spring tides and midday solar exposure (Campbell et al., 2006), are up to 10 °C above the seasonal average (Campbell et al., 2006) and induce mortality (Collier and Waycott, 2014). These event-driven temperature increases may be more detrimental to seagrass than gradual temperature rises, as there is less opportunity for adaptation (Marba and Duarte, 2010).

Climate change is likely to influence the resilience of shallow water seagrass differently from those in deeper water. The higher up the intertidal range the longer the meadow is exposed during low tide to UV, emersion, high temperatures and consequently increased desiccation (Björk et al., 1999). Those seagrasses that are already at (or close to) their physiological limits will be highly impacted by extreme temperature events (Massa et al., 2009; Rasheed and Unsworth, 2011). Furthermore, seagrasses in the intertidal and shallow sub-tidal are affected by the physical impacts of high winds and waves, resulting in actual rapid habitat loss and changes in species composition (Fourqurean and Rutten, 2004; van Tussenbroek et al., 2008).

Those meadows that can resist change through adaptation, or are in a more favourable state to enable recovery are therefore more resilient (Rasheed and Unsworth, 2011; Winters et al., 2011). Factors that promote resilience (e.g., improved water quality, more balanced food web) of these meadows are critical in determining long-term viability. Ultimately, climate change may lead to alterations in the distribution of seagrasses species, and potentially habitat loss or degradation (Short and Neckles, 1999), but improving the resilience of the system by increasing the capacity of the seagrass to resist stress and maintaining the integrity of the important trophic interactions may provide a means of reducing loss or degradation.

4.3.2. Water quality

Decreasing water quality has become so widespread, that it is no longer considered a local, but a regional (De'ath and Fabricius, 2010) or even global-scale ecological management issue (Smith, 2003). Declining water quality is one of the major drivers of accelerating rates of seagrass loss (Lotze et al., 2006; Orth et al., 2006; Waycott et al., 2009) and it is the sensitivity of seagrass to changes in water quality that has earned them the title “*coastal canaries*” sensu (Dennison et al., 1993; Orth et al., 2006).

Eutrophication in aquatic environments generally shifts the competitive balance to faster-growing primary producers. When seagrasses are the dominant primary producers, during the early stages of nutrient loading the plants respond first through an increase in biomass and growth rate, before shifting from structurally large slow-growing species to structurally smaller fast-growing opportunist species (Fourqurean et al., 1995). As loading of the limiting nutrient increases, there is an increase in macroalgae, both free-living and epiphytic, and an associated loss in seagrass, leading to increased sediment anoxia and the dominance of phytoplankton at very high nutrient loadings (Rabalais et al., 2009). This cascade reflects a change from nutrient to light limitation along the eutrophication gradient. Light limitation by elevated suspended sediments is another major factor contributing to water quality based reductions in seagrass resilience (Erftemeijer and Lewis, 2006).

Seagrasses have relatively high light requirements, yet their predominance in coastal habitats exposes them to conditions of low and highly variable light levels that are often impacted by anthropogenic activities (Collier et al., 2011; Dennison, 1987; Waycott et al., 2009). This suggests that seagrass species with lower light requirements would have a competitive advantage. In general, structurally smaller seagrass species have lower minimum light requirements (Erftemeijer and Lewis, 2006), which is thought to be a consequence of their lower respiratory requirements (Duarte, 1991). However, the survival period below the minimum light requirement is shorter in smaller seagrass species because of their lower carbohydrate storage capacity compared to larger species (Collier et al., 2012; Longstaff and Dennison, 1999). Overall, structurally larger seagrass species with a larger below-ground biomass are better adapted to longer periods below minimum light requirements (Erftemeijer and Lewis, 2006).

Apart from nutrients and suspended solids, contaminants such as heavy metals, herbicides, and petrochemicals may also reduce seagrass resilience by impacting energetics, growth and reproduction (Negri et al., 2015). Accumulation of bio-available heavy metals into seagrasses

is widely acknowledged (Sanchiz et al., 2001), however, they can be toxic to seagrass (Macinnis-Ng and Ralph, 2004; Ralph et al., 2006). Heavy metal sensitivity differs between species, although no consistent patterns are apparent and species tolerance to some metals also enables them to recover after acute metal exposure (Prange and Dennison, 2000). It has been suggested that populations may become resistant to metal impacts either through physiological adaptation or genetically based resistance (Macinnis-Ng and Ralph, 2004). Herbicides are another water quality contaminant and the risk is widely acknowledged from agricultural and urban runoff (Flores et al., 2013). Photosystem-II herbicides are the most commonly detected, and these directly affect photosynthetic efficiency, which in turn compromises seagrass health in ways that can be likened to light limitation (Negri et al., 2015). Larger species may rapidly recover after in situ herbicide exposure when returned to uncontaminated water (Macinnis-Ng and Ralph, 2003), but ongoing agricultural application, combined with persistence in the marine environment (half-lives up to 281 d) (Mercurio et al., in press) means that herbicide contamination remains an ongoing threat. Nevertheless, seagrass responses to herbicides and other impacts (such as high light) are additive (Wilkinson et al., 2015) and further research is required to account for their role in cumulative risk and resilience assessments (Ralph et al., 2006).

Improved catchment management can significantly reduce the flow of pollutants to coastal systems, either reversing or abating the trend (Greening and Janicki, 2006). However, if the water and sediment quality improves after loss, as a consequence of the changed sediment condition and predominance of smaller fast-growing opportunistic species, evidence of the recovery to the original state of larger persistent species is scarce (Ralph et al., 2006). With increasing temperature as a consequence of climate change, storage organs, such as the rhizome of the larger slow-growing species have the capacity to become an increasing metabolic burden, and if light becomes insufficient the plants can be driven to a negative carbon balance (Collier et al., 2011). This illustrates the need to maintain good water quality to improve the resilience of seagrasses with increasing climatic change but also highlights that cumulative impacts will exacerbate stressors on seagrass systems.

5. Managing seagrass meadow resilience

Management of seagrass ecosystems needs to undergo a radical change in emphasis and application to improve future resilience. These foundational species have unusually low species diversity and limited structural variability within any single meadow. This presents opportunities for management actions that can be targeted across whole systems consistently. Improving water quality is the most obvious and a relatively rapid initial step to improving seagrass resilience, but this requires consideration of not just the water quality itself but the whole ecosystem and the different features and modifiers that confer resilience upon it (e.g., the presence of a mesograzer community).

The improved ecosystem health and spatial expansion of seagrass meadows as a direct response to increasing sea otter numbers in California highlights how actions to address non-water quality related components of the ecosystem can have significant positive cascades down the food web, enhancing resilience (Hughes et al., 2013). Managing for resilience needs to consider the cumulative impacts of such features as well as modifiers of the system (see Figs. 2 and 4). The specific features and modifiers, as well as the best way to manage them, will differ between different seagrass communities at a variety of spatial scales. The ability to take management action to protect seagrass meadows will be dependent not just on biological and ecological issues but also on a variety of socio-economic factors (e.g., livelihoods, local scientific capacity, stakeholder involvement, availability of funding). Factors such as life-histories, inherently different levels of resilience within the system, variability in the biophysical environment, and variable levels of system fragmentation and isolation all contribute to the need to adapt management at the local scale. Improved understanding and subsequent

Table 2
Potential actions and methods necessary to increase the resilience of a seagrass ecosystem.

Action	Method	Reference
Increase genetic diversity	Deployment of seed buoys (Pickerell et al., 2005) using seeds taken from wider region High diversity in restoration material Enhance genetic connectivity	Jones et al. (2007), Reusch et al. (2005), Reynolds et al. (2013)
Reduce physical impacts	Localised management initiatives (e.g., no anchoring zones, no bait digging). Ensure restoration or recovery of seagrass after damage.	Kenworthy et al. (2006)
Reduce algal/epiphytic overgrowth	Improved water quality and fisheries management of food web	Baden et al. (2012)
Increase photosynthetic productivity	Improved water quality	Dennison (1987)
Reconnect isolated and fragmented meadows	Targeted restoration	Marion and Orth (2010)
Ensure herbivory is balanced	Management of key fishery species and predators through fisheries and habitat management (e.g., MPA's)	Eklof et al. (2008)
Reduced chemical toxicity	Control use and disposal of chemical toxicants in catchment	Haynes et al. (2000)
Provide early warning of issues of concern	Appropriate monitoring of key functional species and groups (plants and fauna)	Green and Bellwood (2009)
Increase compliance with environmental regulations associated to seagrass	Improve local people's knowledge of the value, sensitivity and locality of meadows	Pretty and Smith (2004)
Maintain connectivity	Ensure the health and productivity of associated habitats	Mumby and Hastings (2008)

improved management outcomes for resilience in coral reef systems has been the result of widespread transformational thinking about the relationship between the foundation of the habitat (the corals) and the motile fauna (fish and invertebrates) (Hughes et al., 2010; Mumby and Hastings, 2008). Generating a shift in the strategies adopted for seagrass monitoring and management will require similar transformational changes.

By conducting resilience-based assessments of seagrass meadows, information pertinent to management will be obtainable. Seagrass assessment that goes beyond the traditional metrics of seagrass percentage cover or shoot density is required considering factors that contribute to resilience such as grazing rates, seed banks, or species diversity. This has the capacity to provide information about the chronic, often unseen, drivers of change and hence supporting the development of more targeted policy and associated management actions. Such information can also provide early warning signals of stress, enabling cost-effective action before large scale and expensive restoration is the only remaining option.

A framework for seagrass ecosystem management that centres upon ecosystem resilience requires a hierarchy of management practices starting at the most general and large scale (e.g., catchment and regional scale such as water quality and fishery stock management) and cascading down to smaller meadow-scale issues such as meadow enhancement or restoration and the prevention of anchor or mooring damage (see Table 2). Such measures have the capacity to result in a meadow becoming more or less able to recover from a major climatic impact. An emphasis on promoting ecosystem resilience may result in changes to spatial plans, such as those developed for marine protected areas, in order to focus on protecting key features of resilience.

6. Concluding remarks

Seagrass meadows can survive and remain productive around the world in spite of a changing climate; however for this to happen they must be buffered from other cumulative impacts. Protecting strategies that confer resilience at ecological scales, or re-building resilience in cases of extreme degradation, will provide the best insurance to allow seagrass meadows to remain productive. To improve resilience, sound evidence related to the status of the ecosystem is required. This necessitates data from both contemporary and historical settings, including making use of historical information to source a baseline of what a healthy resilient ecosystem might look like. We need to look beyond mediocre outcomes to develop ambitious plans for ecosystem scale renewal. This can only be achieved by appreciating the value of seagrass meadows and the ecosystem services that they provide. Examples of successful seagrass meadow conservation largely focus on the need to

protect the capacity of seagrass to photosynthesise. While this is clearly important, a highly resilient seagrass ecosystem is one that operates as a largely intact complex food web that contains key functional groups such as herbivores and top predators. Effective management to improve resilience would include measures aimed at water quality enhancement but should equally focus on protecting key functional fauna through the use of marine refugia and fisheries management.

Finally, enabling seagrass meadows globally to help contribute to stabilising our climate, to support our coasts as sea levels rise and to support food security for our growing population requires that their resilience be secured. An agenda of solution based thinking needs to be promoted by placing seagrass ecosystem resilience centrally within the management decision-making process. Further research is required to identify solutions to support the maintenance of key ecosystem services that seagrass meadows provide to our human planet.

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