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Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance

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ABSTRACT

Seagrass ecosystems are inherently dynamic, responding to environmental change across a range of scales. Habitat requirements of seagrass are well defined, but less is known about their ability to resist disturbance. Specific means of recovery after loss are particularly difficult to quantify. Here we assess the resistance and recovery capacity of 12 seagrass genera. We document four classic trajectories of degradation and recovery for seagrass ecosystems, illustrated with examples from around the world. Recovery can be rapid once conditions improve, but seagrass absence at landscape scales may persist for many decades, perpetuated by feedbacks and/or lack of seed or plant propagules to initiate recovery. It can be difficult to distinguish between slow recovery, recalcitrant degradation, and the need for a window of opportunity to trigger recovery. We propose a framework synthesizing how the spatial and temporal scales of both disturbance and seagrass response affect ecosystem trajectory and hence resilience.

1. Introduction

Found at the interface between the land and the sea, seagrasses act as ecosystem engineers by stabilizing sediment, taking up nutrients, storing carbon and providing habitat for fish and other marine fauna (Bos et al., 2007; Jones et al., 1994; Mcleod et al., 2011). The feedbacks

and interactions between seagrass and various biotic and abiotic factors can buffer against stressors, and generate many valuable ecosystem services (Duarte, 2002; Orth et al., 2006a). Seagrass presence can improve conditions for seagrass growth, for example through sediment stabilization, nutrient uptake and sheltering mesograzers (Maxwell et al., 2016). Ironically these feedbacks can also act as a barrier to

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Fig. 1. Seagrass ecosystems are affected by spatial and temporal variability in A) seagrass responses, grouped here as small & fast, intermediate or large & slow. Upscale and downscale processes (red and blue arrows respectively) represent responses at one scale which accumulate to cause changes in processes at higher or lower scales respectively; B) natural processes, for example factors affecting benthic light; C) anthropogenic pressures and D) feedbacks. Full references in Tables S1–S4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recovery: in some cases, the absence of seagrass can render benthic light and sediment stability too low for recolonization (Carr et al., 2010; Nyström et al., 2012; van der Heide et al., 2007; van Katwijk et al., 2009).

The habitat requirements for seagrass have been well characterized, for example as minimum light requirements (Dennison, 1987; Duarte, 1991b), maximum water and current velocity (Cabaço et al., 2010; Infantes et al., 2009), optimum temperature (Adams et al., 2017), and in various seagrass distribution models (e.g. Adams et al., 2015; Grech and Coles, 2010). However seagrass response to environmental change is much more difficult to quantify. Numerous empirical studies have shown that seagrass dynamics are affected by interactions between environmental variables, such as temperature, light and the density and diversity of grazers (Christianen et al., 2012; Collier et al., 2016; Duffy et al., 2003; Eklöf et al., 2010; Heithaus et al., 2014), however these relationships are complex, and laboratory or field manipulations are unable to assess interactions between all variables. Simple

mathematical models demonstrate that self-sustaining feedbacks have the potential to perpetuate either seagrass presence or absence (Carr et al., 2012; Maxwell et al., 2016; Maxwell et al., 2015), but again these models necessarily account for only a small number of processes which affect seagrass dynamics. Large biogeochemical models are able to include more factors, e.g. Baird et al. (2016), but typically cannot include feedbacks by which seagrass influence environmental conditions (Adams et al., 2016) and rely on limited empirical data for parameterization (Adams et al., 2017). Furthermore, as in other environmental systems, the predictive capacity of deterministic models is constrained by limited spatial and temporal resolution of input data (Levin et al., 2012; Oreskes et al., 1994). While a multitude of seagrass indicators exist, no single indicator can provide an overall assessment of condition across a range of scales (Irving et al., 2013; McMahon et al., 2013; Roca et al., 2016). Many indicators are limited in scope outside the specific purpose for which they have been developed, and the relationship between current seagrass state and future condition is

unclear (Kilminster et al., 2015). Establishing causality for seagrass degradation is often difficult, due to the large number of factors involved (Ralph et al., 2007; Walker and McComb, 1992).

Worldwide, seagrass ecosystems face multiple, cumulative anthropogenic pressures (e.g. dredging, trawling, eutrophication, coastal development and climate change) interacting with natural processes over a range of scales (Duarte, 2002; Grech et al., 2012; Orth et al., 2006a; Waycott et al., 2009). Thus there is a need to better understand how seagrass ecosystems respond to disturbance, which we define as any temporary and adverse change to environmental conditions, whether natural and/or anthropogenic in origin (Unsworth et al., 2015). The capacity to undergo disturbance without permanent loss of key ecosystem structures and functions (i.e. “resilience”) is arguably more important than current condition (Holling and Gunderson, 2002). There are two key components of resilience, according to Levin and Lubchenco (2008): resistance to change (including adaptation), and ability to recover.

In this paper, we propose that timescales of resistance and recovery relative to the timescales of disturbance ultimately control the trajectory of seagrass ecosystems. We define four classic trajectories of seagrass degradation and recovery, illustrated by examples from published literature. We also quantify and compare resistance and recovery indicators across 12 seagrass genera. Finally, we introduce a conceptual model to explain how resistance and recovery vary with environmental conditions, spatial and temporal scales of the disturbance, and seagrass condition, population structure and reproductive capacity.

2. Temporal and spatial scales of environmental change and seagrass response

As a biological group, seagrasses have persisted over both ecological and evolutionary timescales in the physiologically challenging submerged marine environment because they have broad realized niches (Carruthers et al., 2007). Seagrass condition at any one point in time gives a snapshot of health according to the chosen indicator (e.g. tissue nutrients, genetic diversity, above ground biomass, spatial extent or connectivity). Current state, however, is not necessarily a good indicator of the resilience of the ecosystem, which depends on resistance, followed by recovery. In the sense of West and Salm (2003) and Levin and Lubchenco (2008), resistance is the capacity of the ecosystem to survive during adverse conditions, which may also involve some adaptation. The degree of degradation caused by a disturbance depends on the resistance capacity, whereas recovery capacity determines if and how degradation is reversed.

The trajectories of degradation and recovery observed in seagrass ecosystems arise from cumulative responses to natural and anthropogenic processes, interacting across a range of temporal and spatial scales (Fig. 1, supporting information in Table S1–4). Processes at molecular to cellular scales respond rapidly to changes in environmental conditions (Fig. 1A). Within meadows, the accumulation of these small, fast processes “upscale” as carbohydrate reserves and other plant-level responses, buffering against medium-term environmental variability. Larger, slower processes at landscape scales stabilise the environment to support regeneration at smaller, faster scales.

To demonstrate how interactions across a range of spatial and temporal scales affect seagrass resistance and recovery, Fig. 1B presents some of the causes of variability in light, a primary driver for seagrass habitat (Dennison et al., 1993; Ralph et al., 2007). When benthic light is reduced (e.g. due to a flood plume or sediment resuspension), photosynthetic yield and other physiological processes adapt almost instantaneously. Changes to cell photosynthetic efficiency, chlorophyll concentration and pigment composition alter the relationship between productivity and light (Ralph et al., 2007), enabling seagrasses to acclimate to changes in light on both short (minutes to days) and long (weeks to months) timescales. At intermediate scales, plant, patch and meadow morphology (plant size, structure and carbon stores) integrate

variations in light over timescales of weeks to months. This provides buffering against short-term stressors, stabilizing the response of molecular and cellular scale processes and underpins meadow development at the landscape scale (Collier et al., 2008; McMahon et al., 2013). Over longer timescales, seagrass condition at intermediate spatial scales (such as shoot density and below-ground biomass) will be affected by the change in carbon production and demand. If light deprivation is severe enough in terms of magnitude, duration and spatial extent, meadow-scale effects may be observed, for example loss of seagrass cover or reduction in area, as shown in the following section.

Anthropogenic pressures modify the nature, timing and scale of natural disturbances, and thus can influence seagrass response to those disturbances as shown by example in Fig. 1C. For example, the characteristics of a flood plume depend on the weather event, natural hydrology and catchment modifications (Waterhouse et al., 2016), and the legacy of dredging, such as ongoing resuspension, will depend on sediment characteristics and local hydrodynamic conditions (Erftemeijer et al., 2006).

Seagrass resistance and recovery are influenced by feedbacks (Maxwell et al., 2016), which also operate at a range of scales (Fig. 1D). At plant or patch scales, seagrass provides habitat for herbivorous grazers, which in turn can reduce epiphyte coverage and hence shading, buffering against eutrophication (Valentine and Duffy, 2006; Whalen et al., 2013). At meadow or ecosystem scales, high grazing pressure can cause a destabilizing feedback for seagrass ecosystems, as decline in seagrass biomass further increases grazing pressure (Christianen et al., 2014; Heithaus et al., 2014).

3. Trajectories of degradation and recovery

Both resistance and recovery occur at a range of scales, ranging from cellular to ecoregion, as shown in Fig. 1. Recovery is typically slower (Roca et al., 2016) and rarely follows the same trajectory as degradation (Duarte et al., 2014). The timescales of degradation and recovery are important, because long-term seagrass absence means the loss of valuable ecosystem services. Furthermore, it can be very difficult to maintain support and funding for management actions if seagrass is absent over long timeframes. For example, the Western Australian Environmental Protection Authorities defines “serious damage” to benthic habitat as damage which is “effectively irreversible or where any recovery, if possible would be unlikely to occur for at least 5 years” (WA EPA, 2016). Thus where recovery takes longer than 5 years, seagrass may be considered permanently lost.

The response of seagrass ecosystems to disturbance can therefore be usefully grouped into four trajectories, based on the timeframe of recovery once the disturbance ends: 1. Rapid recovery (within 1 year); 2. Full recovery within 5 years; 3. Delayed recovery (longer than 5 years); 4. Recalcitrant degradation. Examples of each of these four trajectories are given in Table 1 and Fig. 2, from published studies across a range of latitudes. In the text below, we outline each of these trajectories in greater detail, and explain the significance of spatial and temporal scales of both the disturbance and the seagrass response.

3.1. Degradation at small scales: rapid recovery once disturbance ends

At the smallest scales, degradation can be trivial. For example, photosynthesis is depressed in response to short-term light reduction, and recovers rapidly once the shading ends. Spontaneous recovery in various indicators can also occur for more significant degradation, across the spectrum of seagrass species in locations ranging from tropical to temperate waters. For example, an extensive flood plume in Moreton Bay, Australia caused decline in *Zostera muelleri* starch content, which was rapidly reversed when water quality improved (Fig. 2A, Case study 1 in Table 1).

Table 1
Trajectories of seagrass degradation and recovery.

Case study	Trajectory of degradation and recovery
Degradation at small scales: rapid recovery once disturbance ends 1 – Flood plume decreased starch content in <i>Zostera muelleri</i> , no impact on biomass or meadow extent, Moreton Bay, Australia (Fig. 1A)	Rapid recovery once environmental conditions improved, supported by seagrass integrity at larger scales (Maxwell et al., 2014).
Degradation at meadow to ecosystem scale: full recovery within 5 years 2 – Decadal eutrophication reduced <i>Zostera noltii</i> biomass and extent, Mondego Estuary, Portugal (Fig. 1B) 3 – Cyclone and flood plumes wiped out numerous seagrass meadows (various species) Queensland East Coast, Australia (Fig. 1C–E).	Within 5 years of nitrogen load reduction, biomass increased in remnant meadow, and recolonized adjacent area, recovery ongoing (Cardoso et al., 2010). Gradual recovery of colonizing species over 2–6 years following disturbance. (Campbell and McKenzie, 2004; McKenzie et al., 2016; Rasheed et al., 2014).
Degradation at ecosystem to ecoregion scale: recovery delayed by environmental conditions, 4 – Loss of large, connected meadows of <i>Z. muelleri</i> in Moreton Bay, Australia in 1996 (Fig. 1E) due to water quality deterioration. 5 – Coastal development, dredging and eutrophication over a decade caused widespread seagrass decline Tampa Bay, Florida until 1980s (Fig. 1F)	Recovery first observed in 2011, meadows currently expanding (Dennison and Abal, 1999; EHMP, 2016; Roelfsema et al., 2013) Steady expansion in seagrass area since 1980s, due to water quality improvements, dredging management and restoration (Lewis et al., 1999; Tomasko et al., 2005; Waycott et al., 2009).
6 – Wasting disease (combined with local stressors including water quality and hurricanes) caused widespread <i>Zostera marina</i> loss across the North Atlantic region in 1930s (Fig. 1G–H)	In Denmark, recovery underway by 1950s. In Virginia coastal bays, USA, recovery detected in 1986, restoration from seeding in since 2001 (Orth et al., 2006b): feedbacks and absence of propagules are both implicated in delayed recovery (Carr et al., 2010).
Seagrass loss at ecosystem scale: recalcitrant degradation 7 – Long-term water quality decline caused large-scale loss of <i>Posidonia</i> spp. meadows in Cockburn Sound, Western Australia, while nearby meadows of <i>Posidonia</i> spp. and <i>Amphibolis</i> spp. have been stable on Parmelia Banks, and expanded on nearby Success Banks (Fig. 1I)	Increased nutrients, and light attenuation associated with phytoplankton and epiphyte blooms caused large-scale seagrass loss 1967–1972 in Cockburn Sound. Recalcitrant organic carbon, nutrients and other pollutants and anoxia in sediments inhibits recovery two decades after nutrient loads reduced and light attenuation greatly improved (Kendrick et al., 2002; Walker et al., 2006; Waycott et al., 2009).

3.2. Degradation at meadow to ecosystem scale: full recovery within 5 years

While impairment at physiological scales typically reverses rapidly when conditions improve (Ralph et al., 2002), recovery can take much longer when degradation occurs at intermediate or landscape scales (Collier et al., 2009). And yet there are many examples of decline in seagrass biomass and area, followed by full recovery within a few years (e.g. Fig. 2B–E, Case studies 2–3 in Table 1). Recovery may be immediate, delayed for months or years and/or involve intermediate steps.

In Portugal, biomass of *Zostera noltii* recovered and spatial extent expanded within 5 years of nitrogen load reduction in 1998, after years of decline caused by eutrophication (Fig. 2B, Case study 2 in Table 1). At Abbot Point on the north-east coast of Australia, tropical cyclones in 2008, 2009 and 2011 caused major decline in the biomass of *Halophila* spp. (Fig. 2C, Case study 3 in Table 1). Continuous recovery has been documented for the deep-water meadows since the last cyclone in 2011, however recovery for inshore seagrass did not commence until 2013, with some meadows showing no recovery until 2015 (McKenna et al., 2016). The same three cyclones damaged seagrasses in a mixed meadow further north, on Magnetic Island. While the colonizing species *Halophila ovalis* recovered quickly, return of the previously dominant opportunistic and persistent species (*Halodule uninervis* and *Cymodocea serrulata*, respectively) took almost 5 years for (Fig. 2D). Further south along the east coast of Australia, floods and cyclones during the 1990s caused widespread seagrass loss in the Great Sandy Strait, yet full recovery occurred within only a few years (Fig. 2E).

3.3. Delayed recovery, due to feedbacks and/or limited source material

There are many instances in which seagrass recovers from meadow or ecosystem-scale loss within half a decade, as shown above. In some cases, however, degradation is more persistent. *Z. muelleri* disappeared from Southern Deception Bay in Moreton Bay, Eastern Australia in 1996, with no sign of recovery until 15 years later (Fig. 2E, Case study 4). Another example of slow recovery can be seen in Tampa Bay, Florida, where seagrass area declined by 81% over a century, due to dredging and eutrophication (Case Study 5 in Table 1, Fig. 2F). Seagrass meadows declined from 165 km² in the 1950s to 88 km² by 1982.

Through direct action, restoration, water quality controls and dredging management of Tampa Bay, seagrasses had recovered to approximately 110 km² by the mid-1990s (Lewis et al., 1999).

There are a number of mechanisms which can delay recovery in seagrass habitat. Seagrass loss can cause a change in state, whereby reinforcing feedbacks prevent recolonization, perpetuating seagrass absence (Maxwell et al., 2016; Nyström et al., 2012). The situation is analogous to hysteretic eutrophication in lakes (Carpenter et al., 1999), in that recovery does not commence even once the pressure is removed. Recovery can also be delayed if source material is unavailable: loss of seed banks can prevent recolonization of transitory seagrass meadows (Kilminster et al., 2015; van Katwijk et al., 2010), and absence of new fragments may inhibit recolonization after large scale loss of vegetative seagrass (Orth and McGlathery, 2012). Top predators can enhance recovery rates, through reducing grazing pressure on both seagrass (Heithaus et al., 2014) and on mesograzers which control epiphyte coverage (Hughes et al., 2013): thus changes to coastal food web structure have the potential to reduce seagrass recovery rates.

In practice, it can be difficult to determine whether recovery is delayed by a genuine change in state such that environmental conditions perpetuate seagrass absence, or simply a lack of source material. It is possible that both mechanisms may have impeded recovery from wasting diseases observed in Denmark, and in the Virginia Coastal Bays, USA (Fig. 2G–H, Case study 6). Mathematical modeling suggests that feedbacks perpetuating seagrass absence may have contributed significantly to observed delays in seagrass recovery in the US Virginia Coastal Bays (Carr et al., 2010), but the delay has also been attributed to lack of propagules, due to large scale losses of seagrass across the ecoregion (Orth and McGlathery, 2012). Seagrass meadows in this area reduce sediment resuspension when biomass is high, but low biomass can promote resuspension and thus increase turbidity (Hansen and Reidenbach, 2013). Hence once a meadow becomes established, it can improve local water quality and therefore potentially promote further expansion.

Feedbacks can influence both resistance and recovery, through perpetuating seagrass presence or absence. For example, a feedback between seagrass biomass and water clarity appears to have delayed the recovery of a very large meadow of submerged aquatic vegetation in upper Chesapeake Bay (Gurbisz and Kemp, 2014), and probably

Fig. 2. Examples of different trajectories of seagrass ecosystems, as described in Table 1: A) *Z. muelleri* (Maxwell et al., 2014); B) *Z. noltii* (Cardoso et al., 2010); C) *Halophila* spp. (Rasheed et al., 2014); D) Mixed tropical seagrass (McKenzie et al., 2016); E) *Z. capricorni* in Great Sandy Strait: (Campbell and McKenzie, 2004); *Z. muelleri* in Deception Bay: (Dennison and Abal, 1999; EHMP, 2016; Roelfsema et al., 2013); F) Mixed tropical seagrass (Tomasko et al., 2005; Waycott et al., 2009); G) *Z. marina* (Boström et al., 2003; Frederiksen et al., 2004); H) *Z. marina* (Orth et al., 2006c); I) Mixed temperate seagrass (Kendrick et al., 2002; Waycott et al., 2009).

enhanced recovery rates once recolonization reached a critical threshold. The meadow suffered severe degradation in 1972, with minimal recovery for decades. Water quality improvements associated with a drought in the early 2000s appear to have provided a window of opportunity for the meadow to recover, and as biomass increased, water quality improved. Turbidity was lower inside the meadow, so once the vegetation became established, the bed was able to expand rapidly, even after the drought ended.

3.4. Recalcitrant degradation

Recalcitrant degradation occurs where seagrass recolonization is prevented by feedbacks which perpetuate degraded conditions. Recovery of *Z. marina* in the Dutch Wadden Sea appears to be constrained by a feedback between seagrass, sediment and light (van der Heide et al., 2007). In Adelaide coastal waters, Australia, some meadows of *Posidonia sinuosa* and *Amphibolis antarctica* have recovered after water quality improvements (Bryars and Neverauskas, 2004), but loss in nearby areas be irreversible, due to erosion of substrate.

In Cockburn Sound, Western Australia (Case study 7 in Table 1, Fig. 2I), *Posidonia* spp. meadows were lost due to phytoplankton blooms and nuisance algae, arising from eutrophication. Although these pressures have been greatly reduced since 1979, seagrass area has

continued to decline (Kendrick et al., 2002). In contrast, directly North of Cockburn Sound, recovery of *Posidonia* spp. and *Amphibolis* spp. meadows on Success and Parmelia Banks commenced after improvements in water quality in the late 1970s (Fig. 2I). Cockburn Sound has much less exposure to ocean swells and currents than Parmelia and Success Banks, and the recalcitrant degradation of Cockburn Sound seagrass beds is attributed in part to the restricted flushing and sediment exchange (Walker et al., 2006). Thus Cockburn Sound has been more susceptible to organic enrichment of sediments and the storage and release of historical nutrients, which can be very difficult to reverse (e.g. Valdemarsen et al., 2014).

It is possible that seagrass degradation may appear recalcitrant, when in fact recovery could proceed with source material (seeds or fragments), or through overcoming feedbacks which perpetuate seagrass absence, by either human intervention or natural windows of opportunity. In other cases, recovery proceeds, but very slowly: recovery of large persistent seagrass is predicted to take a century in the Mediterranean, due to the very slow growth rates of these species (Duarte, 1995; González-Correa et al., 2005). In Australia, recovery of *Posidonia* spp. from mooring scars and physical disturbance has taken half a century (Walker et al., 2006). Regardless of the cause, long-term absence of seagrass can be mistaken for, or treated as, permanent loss.

4. Resistance, recovery and seagrass life history strategy

Where resistance time is longer than the duration of the disturbance, seagrass degradation will be minimized. There may be damage at small scales (e.g. consumption of carbohydrate reserves), but live plants are still present at the end of the disturbance and thus recovery can commence (e.g. Case study 1, Fig. 2A). However recovery can be compromised if recurrence time of disturbance is shorter than recovery time. Thus the trajectories of degradation and recovery outlined above depend on the relative timescales of resistance, recovery and disturbance.

Many authors have proposed that timescales of resistance and recovery vary with life history strategy: that large persistent species respond more slowly to change (i.e. have long resistance and recovery times), while smaller, colonizing species both decline and recover more quickly (Duarte et al., 1997; Erftemeijer et al., 2006; Kendrick et al., 2012; Kilminster et al., 2015; Orth et al., 2006a; Roca et al., 2016). Roca et al. (2016) found that the time for indicators to respond to specific stressors were typically longer for measurements at larger organization scale (e.g. landscape scale vs intermediate scale) and for “large” seagrass species. In their experimental study of seagrass burial, Duarte et al. (1997) found that shoot density decline was slowest for the largest species in the study, whereas recovery was fastest for the smaller species.

And yet to date, resistance and recovery have not been quantified across seagrass genera. In part, this is because the timescales of response to environmental change depend on the stressor/s involved (Roca et al., 2016), and the number of potential stressors is extensive (e.g. temperature, salinity, ammonium and sulphide concentrations). Even for any single stressor, the timeframes of resistance and recovery are often not measured directly, can be difficult to compare between studies, and are scale-dependent.

The best estimate we could find of resistance time was survival time during 90–100% light reduction. This indicator can be directly compared between different studies, and has been measured for persistent, opportunistic and colonizing species as defined by Kilminster et al. (2015). Only eight published measurements of survival time under extreme light reduction were found, however, seven of which were for Australian seagrass (Table S5). In absence of any agreed indicator of resistance, and given the limited data available for seagrass survival time under light deprivation, we propose three proxies for resistance based on the hypothesis that resistance is related to plant size: rhizome diameter, shoot weight and total biomass. Data is widely available for each of these three indicators, across 12 seagrass genera, as shown in Fig. 3B–D. The data available for survival time in severe light reduction (Fig. 3A) scales roughly with seagrass size as predicted, ranging from less than one month for the small colonizing species *Halophila ovalis*, up to 2 years for the large, persistent *Posidonia sinuosa* (Fig. 3A–D).

Recovery can proceed via a number of mechanisms, namely sexual reproduction, clonal growth and growth from fragments. In Fig. 3E–G we have plotted three measures of recovery capacity: maximum seed density, horizontal expansion rate and leaf turnover. The ratio of above to below ground biomass ratio is another potential indicator of recovery capacity (Fig. 3H), since above ground biomass provides the capacity for photosynthesis, supporting recovery. As predicted, all four potential indicators of recovery capacity/rate decline with seagrass size (Fig. 3E–H).

A systematic comparison and resistance and recovery capacity is difficult. Survival time (Fig. 3A) is a direct measure of resistance, but it has only been measured in a few studies. While much more data is available for the resistance and recovery indicators shown in Fig. 3B–H, these are all either proxies or only partial measures. Therefore in Fig. 3A we have plotted all of the available data, whereas in Fig. 3B–H only the maximum values for each species are plotted, grouped by genera and sorted according to the classification system of Kilminster et al. (2015). Rhizome diameter was not available for *Ruppia* spp. Four

data points were missing for recovery indicators: seed density for *Enhalus* sp. and *Thalassodendron* spp., and leaf turnover rate for *Ruppia* spp. and *Phyllospadix* spp. Seedling density was used in place of seed density for *Amphibolis* sp., as measured by Verduin, J. (pers. Comm. to KOB, 24/03/2017).

To integrate the information from the different indicators and quantify how resistance and recovery vary between the different seagrass genera, we calculated resistance and recovery capacity, and plotted these by genera in Fig. 4. Since the direct measurements of resistance (i.e. survival time) were available for only eight of the twelve genera, resistance capacity was calculated from the three proxies (rhizome diameter, shoot weight and total biomass). Recovery capacity was calculated from seed density, rhizome extension rate and leaf turnover. The ratio of above to below ground biomass is highly variable, and its role in both resistance and recovery is complex (Hemminga, 1998), therefore it was excluded from the calculation of recovery capacity in Fig. 4.

To quantify and compare resistance and recovery capacity, the maximum value of each resistance and recovery indicator was determined for each genera, and then normalized by the maximum value across all genera. The resistance capacity for each genera was then calculated as the average of the three normalized resistance indicators for that genera, and similarly for recovery capacity. Including or excluding the survival time under low light made negligible difference to Fig. 4, so it was excluded on the basis that the information was available for less than two thirds of the genera. The mean of the three normalized resistance indicators is marked on Fig. 4 for each genera, and the maximum and minimum normalized resistance indicators were used to define the error bars. The same method was applied to recovery capacity. Data used to produce Fig. 4 are provided, with full references, in Tables S6–S7.

Fig. 4 represents the first quantitative comparison of resistance and recovery across seagrass genera. It provides information about the magnitude and variability of both resistance and recovery within and between genera, and illustrates the trade-offs between attributes which promote resistance and recovery in ecosystem foundation species. Investing in sexual reproduction (i.e. recoverability) consumes resources which would otherwise be available to increase biomass and hence resistance capability. High seed density, rhizome extension rates and/or leaf turnover rates can promote recovery but have costs which reduce the ability to survive light deprivation.

Fig. 4 also offers an opportunity to examine in more depth the classifications as proposed by Kilminster et al. (2015) and previous authors. Five out of the six persistent genera have very low values of all recovery indicators (Fig. 4). Maximum seed density, horizontal extension rate and leaf turnover for *Posidonia*, *Enhalus*, *Amphibolis*, *Thalassodendron* and *Phyllospadix* were ≤ 0.2 of the maximum values observed across all species. There was a large range in the resistance capacity across these genera however, ranging from *Posidonia* with the highest total biomass and largest shoot weight, down to *Phyllospadix*, with moderate rhizome diameter and biomass, and low shoot weight (Fig. 3B–D). *Posidonia* are long-lived, slow-growing, large plants which can form extensive long-lived meadows with large standing biomass (Arnaud-Haond et al., 2012). They have strong seasonality in reproduction, and seeds which develop directly, i.e. exhibit no dormancy (Kendrick et al., 2012). Thus the resilience of persistent species is strongly dependent on resisting degradation rather than recovery. The large biomass increases survival time of these species, and may buffer against the impact of some disturbances, e.g. through sediment stabilization, nutrient cycling and wave attenuation (Maxwell et al., 2016). Low recovery rates mean that these species are particularly vulnerable to landscape scale losses, as recovery times can be very long (Duarte et al., 2006).

Thalassia had comparable resistance capacity to the other persistent genera, but higher and more variable recovery capacity, suggesting that it would be more appropriately classified as opportunistic. The survival

Fig. 3. A) Survival time under extreme light reduction (full references in Table S5); B) Rhizome diameter (Duarte, 1991a); C) Shoot weight (Brouns and Heijs, 1986; Duarte, 1991a; Edgar and Robertson, 1992; Ramírez-García et al., 1998); D) Total biomass (Duarte and Chiscano, 1999; Githaiga et al., 2016; Menéndez, 2002; Paling and McComb, 2000); E) Seed density (Kim et al., 2015; Orth et al., 2006b); F) Rhizome extension rate (Duarte, 1991a; Marba and Duarte, 1998; Wortmann et al., 1998); G) Leaf turnover rate (Duarte, 1991a; Vonk et al., 2015); H) Above: below ground biomass ratio (Duarte and Chiscano, 1999; Githaiga et al., 2016). Genera are classified as persistent, colonizing and/or opportunistic as per Kilminster et al. (2015).

Fig. 4. Resistance capacity (based on normalized maximum rhizome diameter, shoot weight and total biomass) and recovery capacity (based on normalized maximum seed density, rhizome extension rate, and leaf turnover). Genera are classified as persistent (triangle symbol), colonizing (star symbol) and/or opportunistic (white fill), as per Kilminster et al. (2015). Thus a genera represented by a back triangle is persistent, white triangle is persistent/opportunistic, black star is colonizing, white star is colonizing/opportunistic, white circle is opportunistic. For data and full references used to construct this figure, see Tables S6–S7.

time measured for *Thalassia hemprichii* and *Thalassia testudinum* under severe light deprivation were comparable with opportunist *Cymodocea serrulata* (Fig. 3A, Table S5). *Thalassia* was also the only genus which had at least one resistance and one recovery indicator > 0.5 of the

maximum values observed across all species. In contrast, the only two genera classified by Kilminster et al. (2015) as purely opportunistic (i.e. *Syringodium* and *Cymodocea*) exhibited low values in both resistance and recovery capacity. *Zostera* overlapped largely with *Cymodocea* and *Syringodium*. *Z. marina* is highly fecund (Orth et al., 2006a) and yet capable of forming large long lived clones, varying its above: below ground biomass ratios, hence is adaptable to a wide range of conditions.

At the other extreme are colonizing seagrass species, *Halophila* spp. and *Ruppia* spp. These seagrasses have low resistance (Fig. 3–4) and low biomass, but the highest recovery rates. *Halophila* spp. possess a broad window of recruitment strategies, and can produce very large numbers of seeds (Fig. 3E), which remain viable for months to years (Kendrick et al., 2012). Thus *Halophila* spp. can recover rapidly from large-scale loss, as shown in Figs. 2C–D. The main threats to these seagrass are therefore interrupted recruitment (e.g. through isolation from other seagrass ecosystems, or damage to seed reserves), or feedbacks which prevent recolonization (e.g. enhanced sediment resuspension or epiphyte coverage in absence of seagrass habitat). For example, *Ruppia tuberosa* in South Australia's Coorong area has recovered very slowly from prolonged disturbance (10 years of drought and hypersalinity) that inhibited replenishment of the seed bank (Kim et al., 2013). Recovery rates might be enhanced by translocation of seed banks from an adjacent, undamaged system which maintain extremely high seed densities (Kim et al., 2015). Thus while colonizing species have high recovery rates, they are not immune to recruitment limitation and recalcitrant decline.

In interpreting Fig. 4, it is important to bear in mind the challenges of quantifying resistance and recovery. Fig. 4 is based on the maximum values of three resistance proxies and three recovery measures found in the literature for each genera, normalized against the maximum overall

values. Thus the figure does not account for the variability within species or genera, which can be substantial, or for the influence of environmental conditions on resistance and recovery processes. For example, rhizome diameters reported by Duarte (1991a) ranged from 1.0 for many species of *Zostera*, up to 5.5 for *Z. asiatica*. Even within a species, each of the resistance and recovery indicators will vary with environmental conditions. For example, rhizome extension rates reported by Marba and Duarte (1998) differed from those reported by Duarte (1991a, 1991b) by > 50% for more than half of the species considered.

5. Putting it all together: a conceptual framework for seagrass trajectories

Resistance and recovery are affected by many factors in addition to the species/genera characteristics, as can be seen from the case studies in Table 1 and Fig. 2. At Abbot Point, deepwater meadows of *Halophila* spp. recovered slowly but steadily after 2011 Tropical Cyclone Yasi (Fig. 2C), but recovery took 4 years longer to commence across shallower sites (McKenna et al., 2016). Water quality decline caused loss of *Z. noltii* meadows on Mondego Estuary, Portugal and *Z. muelleri* meadows in parts of Moreton Bay, Queensland (Fig. 2B, E). In Mondego, seagrass recovery began within a few years of water quality improvement, but the meadow loss in Moreton Bay continued for more than a decade. Thus species/genera alone cannot predict seagrass response to environmental change.

Fig. 5 summarizes some of the key factors affecting resistance and recovery in seagrass ecosystems. Disturbance characteristics, environmental conditions (both past and present) and the presence or absence of feedbacks will influence seagrass condition, population structure and reproductive capacity, as shown in Fig. 5, which in turn affect resistance and recovery timescales a few min.

5.1. Disturbance characteristics

Disturbance intensity, duration, spatial extent, timing and recurrence can affect degradation trajectory. The **characteristics** of the disturbance (e.g. dredging, storm or cyclone, eutrophication or exposure to toxicants) and the **intensity** (e.g. depth of burial, degree of

light reduction, storm intensity, concentration of nutrients or toxicants) influence the resistance time, i.e. how long before damage occurs. For example, the greater the severity of light reduction, the more likely the disturbance will cause biomass decline and damage (Collier et al., 2016; Lavery et al., 2009), and impact seagrass at medium to large scales. If the intensity is low, damage is more likely to be reversible: in some cases, acclimation may even be possible (Ralph et al., 2007).

The **duration** of the disturbance compared to the resistance/survival time will determine the degree of degradation, and the resistance time will depend on seagrass health, environmental conditions and disturbance characteristics (Fig. 5). For example, in cool (23 °C) conditions, it took 1–4 weeks and 4–7 weeks respectively for 90–100% light deprivation to affect the growth rate of *Halodule uninervis* and *Cymodocea serrulata*, but 10–14 weeks and > 14 weeks respectively for shoot density to be affected (Collier et al., 2016). Thus while one month of severe light reduction could be expected to reduce *H. uninervis* growth rates, it would take more than three months to affect the shoot density of *C. serrulata* under these conditions.

The **spatial extent** of the disturbance will influence the scale of degradation, which can be very important for subsequent recovery (Table 1). The larger the area impacted by the event, the greater likelihood that sources for subsequent recovery are compromised, or that large scale self-sustaining feedbacks are lost. Large-scale loss can substantially increase grazing intensity of any remaining seagrass meadow, leading to decline in remnant vegetation as observed in Derawan, Indonesia (Christian et al., 2014).

The **timing** of the disturbance can affect both resistance and recovery. *Posidonia oceanica*, the dominant seagrass in the Mediterranean, can persist over the annual cycle using carbon fixed during only a few months (Alcoverro et al., 2001), and therefore light reduction may have a greater impact on seagrass condition during these critical months. In tropical Australia, differential response to light reduction between growing and senescent seasons has also been found (Chartrand et al., 2016), and recovery from disturbance was found to be lowest during peak growing season in seagrasses on the Chinese coast (Soissons et al., 2016). Where **recurrence time** (i.e. time between disturbance events) is short, the recovery from the previous event may not be complete, meaning subsequent events are more damaging, as shown in Fig. 2C when three tropical cyclones hit Abbot Point over a three year period.

Fig. 5. The trajectory of a seagrass ecosystem in response to disturbance depends on the degree of degradation and recovery, which in turn depend on the relative timescales of resistance, recovery and disturbance. Seagrass condition, population structure and reproductive capacity affect resistance and recovery processes, and are affected by environmental conditions, disturbance history, feedbacks and scale of degradation, as shown.

Importantly, both resistance and recovery are scale-dependent, so the timescales of resistance and recovery will depend on the scale of concern (Fig. 1A).

5.2. Environmental conditions

Seagrass degradation and recovery are affected by environmental conditions (both current and past), seagrass health/reproductive capacity and the presence or absence of feedbacks between seagrass and local biotic and abiotic factors (Fig. 5). Warmer temperatures can reduce survival time for seagrass experiencing light deprivation (Collier and Waycott, 2014; Collier et al., 2016; Collier et al., 2011). Nutrient enrichment can affect resistance and recovery directly, by reducing tolerance to further light reduction (Wazniak et al., 2007) and slowing recovery (Soissons et al., 2014), and indirectly, through influencing species composition (Fourqurean et al., 1995). Direct grazing can increase seagrass resistance to nutrient enrichment (Christianen et al., 2012), but can reduce tolerance to light deprivation (Eklöf et al., 2010) and inhibit recovery (Christianen et al., 2014). Epiphytic grazers can reduce the impact of nutrient enrichment by controlling epiphytic growth (Whalen et al., 2013). Food web structure, including presence of top predators, can influence mesograzers density and seagrass condition (Hughes et al., 2013; Lewis and Anderson, 2012).

5.3. Feedbacks

Feedbacks between seagrass condition (e.g. biomass and area) and biotic and abiotic factors can influence both resistance and recovery, as outlined earlier, but not all feedbacks will be active or important in any given seagrass ecosystem. The feedback between sediment, seagrass and light availability is believed to prevent seagrass recovery in the Dutch Wadden Sea (van der Heide et al., 2007; van Katwijk et al., 2009). However this feedback will have little effect on turbidity in conditions where sediment grain size is either very small or very large, and where plant biomass and water velocity are very low (Adams et al., 2016). Knowing which specific feedbacks are strong in any given context is important for understanding how those feedbacks are likely to affect seagrass degradation and expansion (Maxwell et al., 2016).

Spatial extent of seagrass ecosystems can affect grazing pressure, sediment trapping and nutrient uptake. Thus degradation at landscape scales can impact feedbacks and inhibit recovery. Man-made seagrass restoration is more likely to be successful if the plantings are large scale, so that they can overcome feedbacks perpetuating bare sediment and increase the spatial variability captured within the restoration plot (van Katwijk et al., 2016). For the same reasons, large scale loss reduces the likelihood of natural recovery, due to few available fragments to initiate recovery, and the loss of stabilizing feedbacks. Large scale degradation, or severe degradation in isolated systems, can compromise reproductive capacity and hence recovery due to loss of source materials (Orth and McGlathery, 2012; Rasheed et al., 2014).

5.4. Seagrass condition, population structure and reproductive capacity

The condition and population structure of a seagrass meadow affects both the capacity to survive any given disturbance (i.e. resistance time) and the speed of recovery, as shown in Fig. 5. Seagrass meadows with high genetic diversity, (including multiple species and/or genotypes) are more likely to have individual plants which can tolerate the specific stressor of any given disturbance, and to exploit conditions for recovery (e.g. Hughes and Stachowicz, 2004; Reusch et al., 2005; Reynolds et al., 2012). Healthy carbon stores and growth rates provide a buffer against adverse conditions (Collier et al., 2010), reducing the amplitude of and damage impact occurring during the disturbance, and enabling rapid recovery once conditions improve. The larger the spatial extent of the meadow, the more likely that some portion of the meadow will survive the disturbance, and that seeds or fragments will be available to initiate

recolonization. Healthy trophic cascades within seagrass communities can protect against stressors, for example epiphytic grazers increase light availability and reduce the impact of eutrophication (Whalen et al., 2013). In contrast, absence of top predators can increase direct grazing pressure and remove controls on algal grazers (Heithaus et al., 2014; Hughes et al., 2013), thus increasing the vulnerability of seagrass to other stressors, and reducing capacity for recovery.

Seagrass reproductive health is of particular importance for the recovery process (Kendrick et al., 2012). Greater availability of propagules from a variety of species and clones increases the width range of environmental conditions under which recovery can proceed. Similarly, the size, density, viability and genetic diversity of seed banks all potentially enhance the likelihood of successful recovery (McMahon et al., 2014). Reproductive status is not as well understood as meadow condition however. Observations of recovery require detailed, long term, in situ observations which are not always practical, or possible. This absence of information means that mathematical predictions are restricted largely to changes in abundance/biomass and spatial distribution based on energy budgets (e.g. Baird et al., 2016), or potential distribution based on typical environmental conditions (e.g. Adams et al., 2015; Grech and Coles, 2010).

6. Conclusions

Seagrass ecosystems can take a very long time to recover from degradation, sometimes much longer than management timelines. Meaningful indicators of resistance and recovery are needed, to better understand and predict ecosystem trajectory and response to environmental change.

Author contributions

- Conceived or designed study: KOB; MW; GK; JU; KK; PS; LMCK; KMcM; LR; WD
- Performed research: KOB; PM; MW; GK; JU; AF; KK; PS; LMCK; KMcM; MA; JS-V; ML; WD
- Analyzed data: KOB; PM; MW; GK; AF; MA; JS-V; CC
- Contributed new methods or models: KOB; PM; MW; GK; AF; KK; MA; JS-V; PJM; MC; WD
- Wrote the paper: KOB; PM; MW; GK; JU; AF; KK; PS; LMCK; KMcM; MA; JS-V; ML; MC; WD, CC

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marpolbul.2017.09.006>.

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