Marine Pollution Bulletin xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Review

A framework for the resilience of seagrass ecosystems

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A R T I C L E I N F O

Article history:
Received 23 March 2015
Received in revised form 13 August 2015
Accepted 16 August 2015
Available online xxxx

Keywords:
Conservation
Management
Eelgrass
Meadows
Biodiversity
Connectivity

A B S T R A C T

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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http://dx.doi.org/10.1016/j.marpolbul.2015.08.016
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Please cite this article as: Unsworth, R.K.F., et al., A framework for the resilience of seagrass ecosystems, Marine Pollution Bulletin (2015), http://dx.doi.org/10.1016/j.marpolbul.2015.08.016

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 multispecies 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

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