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Research Note

Testing for thresholds of ecosystem collapse in seagrass meadows

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Abstract: *Although the public desire for healthy environments is clear-cut, the science and management of ecosystem health has not been as simple. Ecological systems can be dynamic and can shift abruptly from one ecosystem state to another. Such unpredictable shifts result when ecological thresholds are crossed; that is, small cumulative increases in an environmental stressor drive a much greater change than could be predicted from linear effects, suggesting an unforeseen tipping point is crossed. In coastal waters, broad-scale seagrass loss often occurs as a sudden event associated with human-driven nutrient enrichment (eutrophication). We tested whether the response of seagrass ecosystems to coastal nutrient enrichment is subject to a threshold effect. We exposed seagrass plots to different levels of nutrient enrichment (dissolved inorganic nitrogen) for 10 months and measured net production. Seagrass response exhibited a threshold pattern when nutrient enrichment exceeded moderate levels: there was an abrupt and large shift from positive to negative net leaf production (from approximately 0.04 leaf production to 0.02 leaf loss per day). Epiphyte load also increased as nutrient enrichment increased, which may have driven the shift in leaf production. Inadvertently crossing such thresholds, as can occur through ineffective management of land-derived inputs such as wastewater and stormwater runoff along urbanized coasts, may account for the widely observed sudden loss of seagrass meadows. Identification of tipping points may improve not only adaptive-management monitoring that seeks to avoid threshold effects, but also restoration approaches in systems that have crossed them.*

Keywords: eutrophication, habitat loss, nutrients, phase shift, tipping point

La Búsqueda de Umbrales del Colapso Ambiental en las Praderas de Pastos Marinos

Resumen: *Aunque el deseo público por un ambiente saludable es más que claro, la ciencia y el manejo de la salud de los ecosistemas no han sido sencillos. Los sistemas ecológicos pueden ser dinámicos y pueden cambiar súbitamente de un estado ambiental a otro. Dichos cambios impredecibles suceden cuando se cruzan los umbrales ecológicos; esto es, pequeños incrementos acumulativos de un estresante ambiental conllevan a un cambio mucho mayor del que podría pronosticarse a partir de efectos lineales, sugiriendo que se ha cruzado un momento crítico imprevisto. En las aguas costeras, la pérdida de pastos marinos a gran escala ocurre comúnmente como un evento repentino asociado con el enriquecimiento de nutrientes causado por humanos (eutrofización). Probamos si la respuesta de los ecosistemas de pastos marinos al enriquecimiento costero de nutrientes está sujeta al efecto umbral. Expusimos lotes de pastos marinos a diferentes niveles de enriquecimiento de nutrientes (nitrógeno inorgánico disuelto) durante diez meses y medimos la producción*

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neta. La respuesta de los pastos marinos exhibió un patrón de umbral cuando el enriquecimiento de nutrientes excedió niveles moderados: hubo un cambio mayor y súbito de positivo a negativo de producción neta de hojas (de aproximadamente 0.04 de producción de hojas a 0.02 de pérdida de hojas por día). La carga de epífitas también incrementó conforme incrementó el enriquecimiento de nutrientes, lo que pudo haber conducido el cambio en la producción de hojas. Cruzar dichos umbrales de manera inadvertida, como puede ocurrir por medio del manejo inefectivo de contribuciones derivadas del suelo como las aguas negras y la escorrentía de lluvia a lo largo de las costas urbanizadas, puede representar la pérdida de praderas de pastos marinos observada ampliamente. La identificación de los momentos críticos puede mejorar no sólo el monitoreo del manejo adaptativo que busca evitar los efectos umbral, sino también las estrategias de restauración en sistemas que ya han cruzado estos umbrales.

Palabras Clave: cambio de fase, eutrofización, momento crítico, nutrientes, pérdida de hábitat

Introduction

The concept of ecological thresholds emerged in the 1970s from theoretical models and empirical observations of dramatic changes in ecosystems (Holling 1973; May 1977). It suggests ecological systems are susceptible to abrupt change (e.g., in quality or property), and small changes in environmental conditions produce large responses (Groffman et al. 2006; Suding & Hobbs 2009). When a threshold is recognized the stressor can be managed (e.g., nitrogen pollution) such that it does not exceed the point past which change is observed. Where they are unknown, small shifts in environmental stressors could elicit unexpected ecosystem change (e.g., grasslands to woodlands and coral- to algal-dominated systems) (Scheffer et al. 2001). Although threshold effects are well established in theory (Groffman et al. 2006; Suding & Hobbs 2009), they are poorly validated in the field. The major research challenge is to identify when systems are approaching their tipping point, a critical precursor to predicting loss (i.e., early warning signals, Scheffer et al. 2009) and the stabilizers against loss (i.e., the system's capacity to resist) (Connell & Ghedini 2015). This feeds into the ultimate goal of improving monitoring for adaptive management and determining whether management goals are being met (Groffman et al. 2006).

Seagrass meadows are renowned for providing critical ecosystem services and habitat for marine species (Orth et al. 2006). Catastrophic losses in seagrass meadows have been documented worldwide over recent decades (Waycott et al. 2009) and are often characterized by the sudden unexpected disappearance of entire meadows (e.g., Cambridge & McComb 1984). This sudden loss of seagrass is often linked to heavy nutrient loading (i.e., eutrophication) in coastal waters (review by Burkholder et al. 2007), which drives a self-accelerating cascade of direct and indirect effects commonly associated with excessive epiphyte proliferation (Walker & McComb 1992; Duarte 1995; Mabrouk et al. 2013). But, their susceptibility to threshold effects is unknown. These effects can overpower buffering processes that maintain resistance so that loss is sudden rather than gradual. This leads to the question of whether this sudden loss is a result of seagrass surpassing a threshold in response to increasing nutrient load.

Considerations of threshold effects have rarely moved beyond the development of theory to test in the field. The sudden loss of seagrass meadows suggests there is a threshold effect and represents a case that can be used to validate their existence *in situ*. We tested whether a gradual increase in environmental stress leads to gradual decline or sudden loss (i.e., threshold effect). Specifically, we investigated whether incremental increases in nutrients and associated epiphyte cover cause a proportional reduction in net productivity of seagrass meadows or whether there is a threshold effect beyond which the magnitude of change is considerably greater.

Methods

We tested the hypothesis that seagrass switch from growth (net production of leaves) to decline (net loss of leaves) across a gradient of nutrient enrichment on a naturally nutrient-poor coast by exposing plots of *Amphibolis antarctica* (20 × 20 cm) to 7 levels of controlled nutrient enrichment for 10 months ($n = 5$ replicate plots per enrichment level) (Supporting Information), which enabled seasonal variation to be encompassed. The seagrass plots were located 4–6 m deep and 2 km offshore from Lady Bay, Fleurieu Peninsula, South Australia (35°27′44.4132″ S, 138°16′9.138″ E), where background measures of dissolved inorganic nitrogen (DIN) were below detection limits (0.001 mg/L). Using well-established methods (McSkimming et al. 2015), we wrapped varying weights of fertilizer (Osmocote Pro, Scotts, Australia) in nylon mesh bags and secured them at substrate level with plastic stakes (see Supporting Information for translation of fertilizer weight to DIN concentrations in the field). Plots were separated by a minimum of 2.0 m to ensure independence of enrichment, based on a previous field-trial that showed background concentrations occurred within at least 0.5 m of such bags of Osmocote (Scotts, Australia). The fertilizer within bags was replaced at 10-week intervals to ensure continuous enrichment.

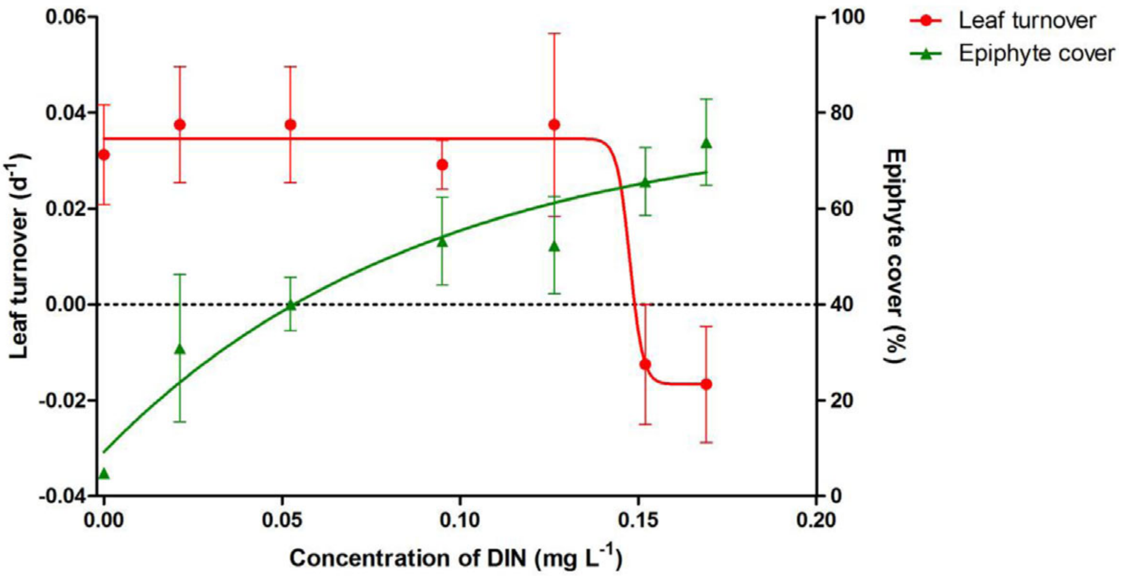

*Figure 1. Leaf turnover (leaf production minus leaf drop) and epiphyte cover (mean [SE]) of seagrass (*Amphibolis antarctica*) exposed in situ to increasing levels of nutrient enrichment (DIN, dissolved inorganic nitrogen). The modeled curves are based on the dose-response model (Berry & Wallace 1981).*

As a proxy measure of seagrass persistence, we measured net production (i.e., leaf turnover) *in situ* as the product of leaf production minus leaf drop (see Methods in Walker [1985]). *Amphibolis antarctica* has a number of shoots with leaf clusters (typically 10–12 leaves each) that extend from each vertical rhizome. It grows by continually developing new leaves at the apex of each leaf cluster and drops older leaves as it grows (see Marbà & Walker 1999). To quantify leaf production, a nylon-cable tie was placed above the fifth leaf from the top of a meristematic apical leaf cluster ($n = 2$ leaf clusters per plot), and the number of leaves above the tie were counted after 10 months. To quantify leaf drop, we affixed ties above the fifth leaf of different clusters ($n = 2$ leaf clusters per plot), and counted the number of leaves below the tie. The percent cover of epiphytes on leaf surfaces was estimated from randomly selected individuals ($n = 5$ per plot). We divided the fifth youngest leaf from the apical tip into 1 mm^2 cells and recorded each cell as either covered or not covered with epiphytes. We used analysis of variance to test for differences among the seven levels of enrichment and post hoc pairwise tests to identify which of these levels differed from each other (Supporting Information).

Results

Seagrass exhibited a threshold response to nutrient enrichment. A cumulative increase in nutrients from 0 to 0.13 mg/L of DIN resulted in little change in leaf turnover, but past this enrichment level, further increases in nutrients resulted in a switch from net seagrass production to net seagrass loss (Fig. 1). The switch from positive to negative leaf turnover occurred when leaf drop increased; leaf production remained relatively stable under all levels of nutrient enrichment (Supporting Information). Hence, a threshold effect was evident (between 0.13 and 0.15 mg/L of DIN) as seagrass switched from growth (net production of leaves) to decline (net loss of leaves). The cover of epiphytes on seagrass leaves increased gradually with increasing nutrient enrichment (Fig. 1); leaves had approximately 50% coverage at the point the threshold effect was observed.

Discussion

We experimentally demonstrated that a gradual increase in environmental stress (i.e., nutrient loading) drove a switch from net seagrass production to net seagrass loss. Seagrass remained unaffected during gradual increases in nutrient pollution (minor to moderate enrichment), but then small cumulative increases in nutrients drove a much greater consequence than would be predicted from linear effects (Fig. 2). Hence, an unforseen tipping point was crossed. The point at which the threshold effect was manifest in our test system suggests that seagrass meadows are resistant to moderate DIN enrichment (i.e., terrestrial runoff from natural and agricultural catchments), but not major enrichment (i.e., urban catchments) (Fig. 2). In our study, minor to moderate nutrient enrichment reflected terrestrial inputs from natural and agricultural catchments and major enrichment reflected inputs

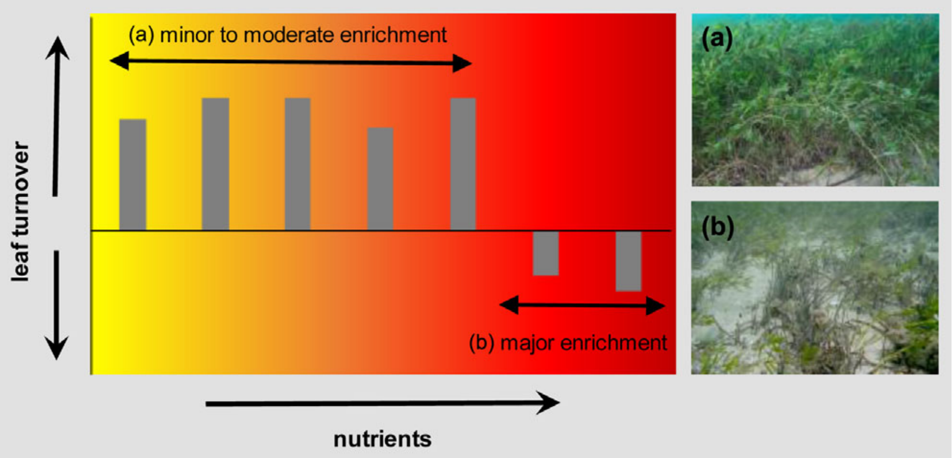

Figure 2. Response of seagrass meadows (i.e., leaf turnover) to increasing nutrient enrichment (i.e., dissolved inorganic nitrogen concentration): (a) minor to moderate levels of enrichment (ecosystem persistence) and (b) small cumulative increase in nutrients (moderate to major levels) that elicit a threshold effect (ecosystem loss).

from heavily populated urban catchments (Gorman et al. 2009; McSkimming et al. 2015).

Although the mechanisms by which nutrient pollution drives seagrass loss is impressively documented (reviewed in Burkholder et al. [2007]), the existence of tipping points changes thinking on management of these systems. Nutrients are essential for seagrass photosynthesis and growth (i.e., they are a resource), but at elevated levels they suppress net productivity. Beyond a particular level of nutrient availability, further enrichment may no longer support net production, but rather may result in a negative turnover rate as the balance between leaf production and drop is disrupted.

Good quality coastal water is a highly valued resource, worth hundreds of millions of dollars in Australia alone (e.g., MacDonald et al. 2015). Ongoing economic decisions pivot on the balance between the financial acceptability of nitrogen-reduction targets (i.e., taxpayer burden) and ecological outcome relative to thresholds (i.e., targets do not over or under deliver ecological improvements). The difficulty is that managers can unwittingly push a system to the brink whereby stressors continually increase without signs of stress, and then suddenly an unrealized threshold is exceeded that leads to a catastrophic outcome (Foley et al. 2015). In our example, a threshold occurred with *Amphibolis antarctica*, a species that forms extensive seagrass meadows in temperate Australia (Edgar 1997). By recognizing this threshold effect (i.e., knowing the point where excess nutrients have the greatest impact), one can begin to manage for it and minimize socioeconomic cost. Thereby, the management of nutrient pollution at minor to moderate levels would enable persistence of seagrass systems and their ecosystem services (e.g., nutrient absorption).

Resource enrichment (e.g., nitrogen from terrestrial runoff or carbon from fossil fuel combustion) represents a persistent enigma for those who manage biogenic habitats because enrichment often acts as a direct positive effect (i.e., resource [Burkholder et al. 2007; Connell et al. 2017]), but it also has an indirect negative effect (i.e., stressor [Burkholder et al. 2007; Connell et al. 2013]) where it favors fast-growing and opportunistic competitors (Vitousek et al. 1997). The stressor most commonly argued or demonstrated for seagrass loss by nutrient over enrichment is light reduction through stimulation of high-biomass algal overgrowth as epiphytes (Burkholder et al. 2007). We found that epiphyte overgrowth increased gradually with gradual increases in enrichment, suggesting the mechanisms that drive loss (e.g., light reduction) may mediate the threshold effect. Yet, in many seagrass systems, the reason for the sudden nature of change may be as much about tipping points in photophysiology associated with epiphytic growth (Bulthuis & Woelkerling 1983; Gurbisz & Kemp 2014) as it is about the sudden loss of ecological buffering processes that mediate their growth (i.e., trophic compensation [McSkimming et al. 2015]).

Although enrichment stimulates rapid growth of algal epiphytes, there appears to be a tipping point past which grazers can no longer control algal biomass on seagrass (Wetzel & Neckles 1986). In response to enrichment, herbivores can increase consumption of high-quality algae (Falkenberg et al. 2014) and expand their population size (Heldt et al. 2016) to buffer against such enhanced algal production (McSkimming et al. 2015). Such compensatory effects stabilize a system as disturbances intensify, but their collapse drive a self-accelerating cascade of direct and indirect effects (Duarte 1995) and sudden loss of resistance (Connell & Ghedini 2015). Hence, a persistent challenge to identifying thresholds, the point at which resistance is lost, is the detection of compensatory processes where the masking effects are immediate and result in no observable change. In most circumstances, ecosystems often appear stable because of their natural inherent resistance to environmental change (Ghedini & Connell 2016), but where compensatory processes fail to counterbalance the effect of change, the result may be unpredictable phase shifts from one state to another.

Hence, not all meadows will be subject to loss because of spatial differences in stabilizing processes of ecosystems that compensate for increasing effects of multiple disturbances (Ghedini et al. 2015).

The idea that ecosystems can switch abruptly to a contrasting state is widely accepted (Scheffer et al. 2001), yet because its inception, based on theoretical models (Holling 1973; May 1977), these phase shifts have been rarely documented. Although predicting threshold effects is notoriously difficult, because of a multitude of interacting processes that operate over very different scales of space and time, we identified a tipping point relevant to catchment management. By identifying these threshold effects, we sought to account for the widely observed sudden loss of seagrass meadows and to inform ongoing managerial judgments that necessarily balance financial acceptability of nitrogen-reduction targets with outcomes sought by the public.

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Supporting Information

Information on how experimental DIN loads compared with real-world catchment DIN loads (Appendix S1), results of analyses of the effect of enrichment on leaf production and drop, leaf turnover, and epiphyte cover (Appendix S2), and a graphical representation of leaf production and drop at each DIN concentration (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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