

# Reversal of intraspecific interactions by an ecosystem engineer leads to variable seedling success along a stress gradient

S. Yang<sup>1,2,\*</sup>, J. HilleRisLambers<sup>1</sup>, J. L. Ruesink<sup>1</sup>

<sup>1</sup>Department of Biology, University of Washington, Box 351800, Seattle, WA 98195-1800, USA

<sup>2</sup>Present address: Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221, USA

**ABSTRACT:** By definition, ecosystem engineers can have large effects on resource flows and habitat structure, with impacts on other organisms ranging from facilitative to inhibitory. The stress gradient hypothesis posits that facilitative interactions predominate in conditions of environmental stress and switch to competitive interactions in benign environments. We conducted an empirical test of the stress gradient hypothesis for a marine ecosystem engineer, eelgrass *Zostera marina* L., across a hydrodynamic gradient. Eelgrass meadows perform important functions in coastal ecosystems and have experienced contemporary declines worldwide with variable recruitment success. In this study, we first determine whether eelgrass modified the local hydrodynamic conditions and then how the presence of an adult eelgrass canopy affected the plants' own relative seedling success over the hydrodynamic gradient. Eelgrass reduced water motion significantly, which provided a positive feedback on survival and growth for conspecific seedlings, but only at the stressful end of the hydrodynamic gradient. By contrast, adult conspecifics negatively impacted seedling recruitment and growth in calmer environments, presumably due to intraspecific competition. Thus, eelgrass ecosystem engineering does not always facilitate the plant's own performance, and our results support the stress gradient hypothesis as an explanation for this context dependence. The balance of these complex interactions may provide a mechanism for delayed or failed recovery of eelgrass in habitats exposed to high hydrodynamic exposure.

**KEY WORDS:** Context dependence · Density dependence · Habitat modification · Seagrass · Stress gradient hypothesis

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Organisms that are physical 'ecosystem engineers' alter resource availability through mechanisms other than competition and predation, namely, by modifying the physical environment (Jones et al. 1994, 1997, Odling-Smee et al. 2003). Numerous case studies from a variety of systems demonstrate wide-ranging impacts of ecosystem engineers: from both positive to negative and strong to weak (Jones et al. 1997). For

example, shrubs facilitated colonization of an oak species by producing shady microsites suitable for recruitment (Callaway 1992), whereas invasive cordgrass *Spartina* sp. produced tall, dense canopies, excluding native organisms from coastal marine habitats (Lambrinos 2007). Curiously, the same ecosystem engineer can have varied effects in different contexts. For instance, iceplant *Carpobrotus edulis* can change soil pH and calcium, but the magnitude of the change depends on the ecosystem in which it lives,

\*Corresponding author: sylvia.yang@wwu.edu

such as grassland or coastal scrub (Molinari et al. 2007).

The strength of ecosystem engineering may depend on environmental context (Byers et al. 2006, Cuddington et al. 2009). One specific manifestation of this context dependence appears in the stress gradient hypothesis, which predicts a preponderance of facilitative interactions under conditions of high environmental stress and negative interactions in more benign environments (Bertness & Callaway 1994, Bruno et al. 2003, He et al. 2013). Thus, if ecosystem engineers have their signature physical effects on an environmental factor (i.e. those that define them as 'engineers') through facilitative interactions, they should have their strongest impacts in harsh physical environments where they ameliorate conditions stressful to other organisms (Crain & Bertness 2006) or themselves (Cuddington & Hastings 2004). The effects of ecosystem engineers have been demonstrated to be context-dependent for a population of a single species through theoretical modeling (Cuddington & Hastings 2004, Cuddington et al. 2009), and for terrestrial and aquatic communities through experiments (Molinari et al. 2007, Daleo & Iribarne 2009, Scyphers & Powers 2013, Green & Crowe 2014). The stress gradient hypothesis provides a way of making predictions when either the environment shifts in stress or the ecosystem engineers shift in abundance, thus aiding conservation and restoration (Cuddington & Hastings 2004, Suding et al. 2004).

Seagrasses, submerged marine angiosperms, are recognized as ecosystem engineers and have been a focus of conservation efforts. Amongst many other ecosystem functions, seagrasses act as biogenic habitat for many species, such as juvenile stages of harvested species (Heck et al. 2003), and are sensitive to human impacts (Short & Wyllie-Echeverria 1996). Natural and anthropogenically caused declines of seagrasses worldwide have been called 'a global crisis' (Orth et al. 2006), with restoration attempts having mixed success. Human-aided restoration methods employ the addition of seed as well as clonal proliferation of adult shoot transplants, with approximately 40% success (Fonseca et al. 1998). Recolonization by seeds and seedlings has been a successful restoration strategy at some locations (e.g. McGlathery et al. 2012, Orth et al. 2012) and is especially critical at large denuded sites (e.g. Lee et al. 2007). Yet, seedling survival through the first year tends to be low at many sites (e.g. <1% in Odense Fjord: Greve et al. 2005), but high in others (e.g. ~16 seedlings m<sup>-2</sup>:

Plus et al. 2003; ~85 seedlings m<sup>-2</sup>: Lee et al. 2007). Factors that have been suggested to drive this variability in restoration success include timing of germination, burial (Marion & Orth 2010), temperature, oxygen, salinity, bioturbation, grazing, hydrodynamic disturbance (Greve et al. 2005), and lack of an adult seagrass canopy (Lee et al. 2007).

Ecosystem engineering by the seagrass *Zostera marina* L. (eelgrass) has the potential to impact the establishment of its own seedlings, influencing the management and restoration of this important species. Eelgrass is not in decline everywhere (e.g. Gaeckle et al. 2011), and it is often uncertain why some populations succeed while others fail. The stress gradient hypothesis could provide insight into context-dependent processes that facilitate or prevent recovery for this species (e.g. van der Heide et al. 2007). Waves and currents ('hydrodynamic' conditions) negatively affect eelgrass distribution (Fonseca & Bell 1998) and seedling recruitment (Koch et al. 2010, Valdemarsen et al. 2010). However, meadows of eelgrass can ameliorate hydrodynamic energy (reviewed in Koch et al. 2006). Thus, eelgrass has the potential to facilitate its own recruitment through mitigating hydrodynamic conditions that might erode seedlings away, but it is unclear how strong this engineering is compared to overlying variation in hydrodynamic conditions (i.e. the stress gradient).

In this study, we tested the stress gradient hypothesis as a framework for variable eelgrass seedling survival over a hydrodynamic gradient. We manipulated eelgrass shoot density along a hydrodynamic gradient and determined (1) how eelgrass modified water motion along and relative to the gradient, (2) how the overlying gradient in water motion affected seedling survival, and (3) whether and how the presence of adult eelgrass shoots affected seedling survival and performance. We hypothesized that higher seedling mortality would occur at the end of the gradient with greater water motion due to erosive dislodgment. Aligning with the stress gradient hypothesis, we predicted that eelgrass would facilitate seedling recruitment and growth in habitats with higher water motion because an eelgrass canopy could decrease water motion in these more stressful environments. By contrast, we predicted that high eelgrass density would have negative or neutral effects on adult eelgrass survival, seedling recruitment, and growth in calmer environments, where the benefits of such facilitative interactions should be outweighed by competitive interactions.

## MATERIALS AND METHODS

### Field site

Willapa Bay, WA, USA is a mesotidal, partially mixed estuary (Banas et al. 2004) with ~10% of its total area containing *Zostera marina*. Our study site was located on the west side of the Bay, approximately 1 km from shore, on intertidal hard sand substrate (46.522°N, 124.014°W). We selected this site because it included a gradient of eelgrass from continuous meadow at the north end of the site to sparser eelgrass at the south end of the site, which we expected to reflect a hydrodynamic gradient (Baden & Boström 2001) established by beach slope and aspect (Fig. 1).

### Experimental design

In May 2010, we set up 20 experimental blocks, with 3 treatment plots in each block. The blocks were arrayed at approximately 50 m intervals along the assumed hydrodynamic gradient at a common tidal elevation (0 m relative to mean lower low water [MLLW]). Each plot was 4 m<sup>2</sup>, randomized, and spaced 2 m apart in each block. In the 'ambient' treatment plots, eelgrass was not manipulated, so the plots simply contained shoots at naturally occurring densities, which varied from 0 to 132 shoots m<sup>-2</sup>. In the 'addition' plots, eelgrass was transplanted into (or removed from) the center 1 m<sup>2</sup> to achieve a consistent density of 120 shoots m<sup>-2</sup>. In the 'removal' plots, all eelgrass shoots and rhizomes were removed from the entire plot (0 shoots m<sup>-2</sup>) (Fig. 1).

To verify the assumed hydrodynamic gradient and estimate the effect of eelgrass on hydrodynamic conditions, we deployed dissolution blocks within each treatment plot. This method allowed for simultaneous measurement of relative water motion in each of the 60 plots over the spatial gradient, often within dense eelgrass canopies, which would not be feasible with

digital current meters. Dissolution blocks (12 cm<sup>3</sup>) were made of plaster of Paris with a wire (12 gauge, 20 cm long) inserted into each block before hardening. Blocks were dried (60°C) and weighed prior to and after field deployment. Two blocks were inserted into each plot, wire-first into the sediment with the block flush with the sediment surface (Porter et al. 2000), for 2 full tidal cycles (2 d) in June 2010. Greater plaster loss indicated greater mass transfer due to more vigorous water motion (Thompson & Glenn 1994, Porter et al. 2000).

We separately verified that plaster loss was related to the hydrodynamic water regime. Specifically, we deployed dissolution blocks at set depth

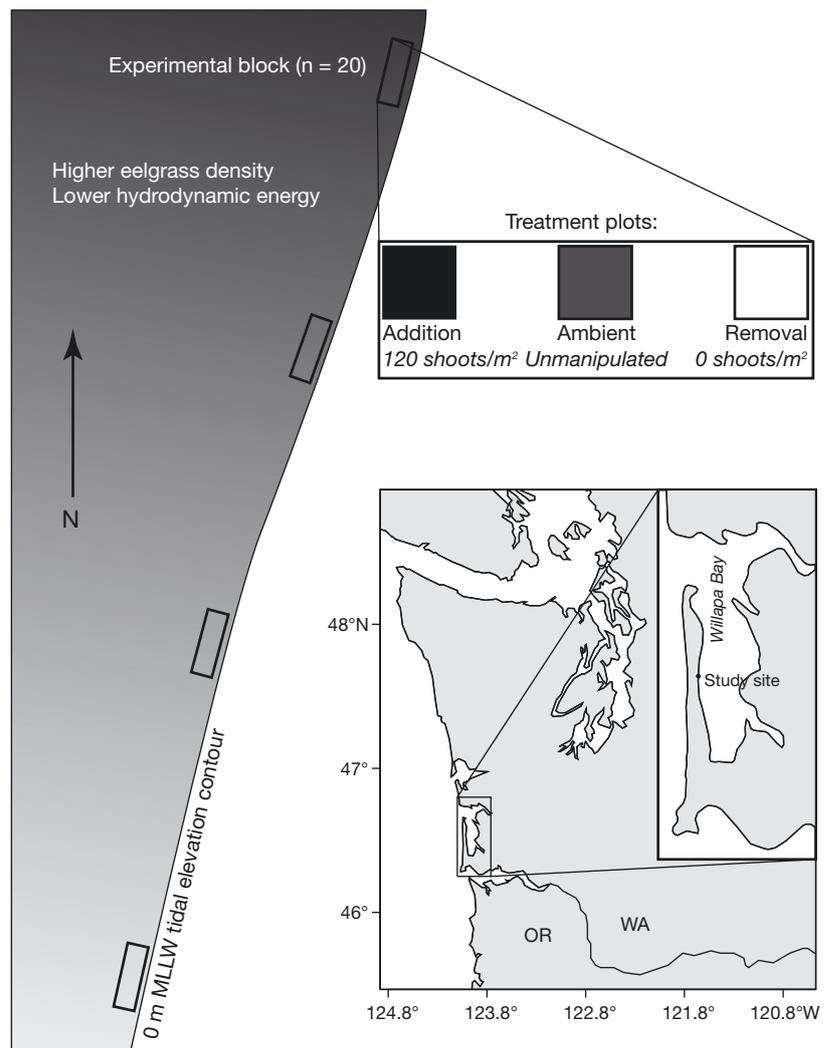


Fig. 1. Schematic diagram (left) of the intertidal showing an existing gradient of eelgrass (*Zostera marina*) density and hydrodynamic energy (grayscale) and 4 example blocks of the experimental design (see 'Materials and methods'). Inset lower right: location of study site. MLLW: mean lower low water

intervals in the boundary layer concurrently with acoustic Doppler current profilers (Aquadopp Profiler, Nortek) at the same field site in areas denuded of eelgrass. These measurements verified that there is a linear relationship between kinetic energy and the amount of plaster dissolved ( $n = 16$ ,  $R^2 = 0.48$ ,  $p = 0.0018$ ): Plaster dissolved ( $\text{g d}^{-1}$ ) =  $322.98 \times \text{Kinetic energy (m}^2 \text{ s}^{-2}) + 7.82$ . Since plaster dissolution can vary somewhat with water temperature, salinity, and other environmental factors that fluctuate in the field, we consider this calibration equation as an estimate. We report mass transfer, a metric reflecting unidirectional and oscillatory flow integrated over time, as the amount of plaster dissolved, and hereinafter refer to it as 'water motion.'

To evaluate the impact of the presence of eelgrass on seedling performance, we focused on adult shoot density in the center  $1 \text{ m}^2$  of each plot and performance of 25 seedlings transplanted 10 cm apart in a square grid in the center  $0.25 \text{ m}^2$  of each plot. Adult shoots and seedlings were counted at the beginning (May), middle (June and early July), and end of the experiment (end of July). At the end of July (2010), we destructively sampled the center  $0.25 \text{ m}^2$  of each plot because the aboveground portion of the seedlings had grown to be morphologically indistinguishable from adult vegetative shoots. Seedlings were identified by their short 'scorpioid' rhizome and were measured for shoot size and rhizome branching. All eelgrass adult shoots and seedlings transplanted into the plots originated from the north end of the gradient to control for differences in shoot morphology along the gradient.

### Statistical analyses

To determine the gradient of environmental conditions experienced in the experimental plots and the impact of adding or removing eelgrass, we used a generalized linear mixed effects model in R (R Development Core Team 2011), with water motion (amount of plaster dissolved) as the response variable, eelgrass treatment (ambient, addition, removal) and distance of experimental block along the north to south transect as the fixed effects, and plot as the random effect. We used pairwise likelihood ratio tests (LRT) between the full model and models with each of the main effects and interaction removed to identify statistically significant explanatory variables. Furthermore, we used the average plaster dis-

solved in the removal treatment plot of each experimental block to represent the overlying water motion without any influence of eelgrass engineering in that block.

To test whether the presence of adult eelgrass shoots facilitated retention of seedlings, we used generalized linear models (GLM) with Poisson or binomial error structures as appropriate, using adult eelgrass shoot density and seedling survival as the response variable and eelgrass treatment and water motion (amount of plaster dissolved) as the explanatory variables. Analysis of adult density data was limited to the ambient eelgrass and eelgrass addition treatments because the eelgrass removal treatment had no eelgrass shoots and therefore does not provide useful data points. For seedling survival, we limited the comparison to the eelgrass addition and eelgrass removal treatments, since ambient plots varied in adult eelgrass shoot density ( $0\text{--}132 \text{ shoots m}^{-2}$ ). We then tested for intraspecific effects on morphological characteristics (shoot length, sheath width, number of branches, and number of rhizome internodes) of all seedlings surviving to the end of experiment using generalized linear mixed effects models, using plot as the random effect and associated error structures. We used LRTs to determine significance of each main effect and generalized linear hypothesis testing to conduct post hoc comparisons amongst the treatment groups.

## RESULTS

### Strength of eelgrass engineering relative to existing hydrodynamic environment

Water motion was decreased by eelgrass addition and also varied with distance along the north–south transect (representing a hydrodynamic gradient; Fig. 2, linear mixed effects model,  $p < 0.001$  for both variables); however, the interaction was not significant ( $p = 0.21$ ). Over the north–south gradient (Fig. 1), greater water motion occurred on the southern end, with the most water motion in plots with eelgrass removed. Plots with eelgrass removed ( $0 \text{ shoots m}^{-2}$ ) consistently had  $2.41 \text{ g}$  more plaster dissolved than plots with eelgrass added ( $120 \text{ shoots m}^{-2}$ ) (Fig. 2b). This decrease in water motion by eelgrass' engineering was 28% of the range of water motion experienced over the gradient in the removal plots ( $8.55 \text{ g}$  plaster dissolved).

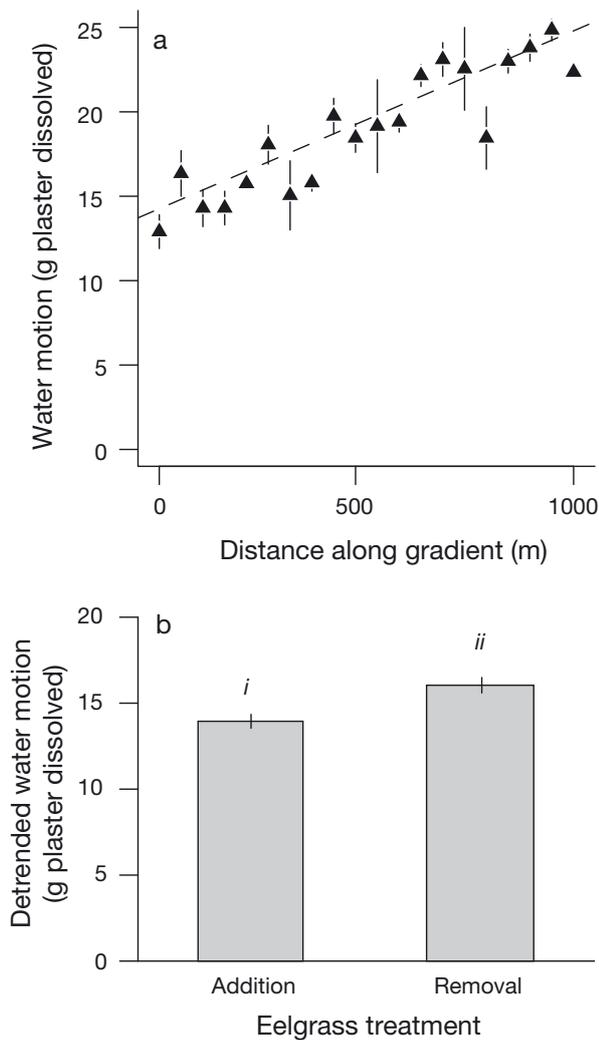


Fig. 2. (a) Demonstration of the natural, overlying hydrodynamic gradient along the experimental transect in unmanipulated eelgrass (*Zostera marina*) densities. Error bars depict standard error. (b) The hydrodynamic condition, modified by the addition of eelgrass to a constant density (120 shoots  $m^{-2}$ ) or the complete removal of eelgrass (0 shoots  $m^{-2}$ ), detrended to remove the overlying gradient. Different roman numerals indicate significant differences ( $p < 0.05$ )

### Adult eelgrass density manipulation

At the end of the experiment (July 2010), both ambient and eelgrass addition plots maintained higher adult shoot densities in plots with lower water motion (Poisson GLM, mass transfer effect,  $p < 0.0001$ ) (Fig. 3a). However, final density in addition plots was higher than that of the ambient unmanipulated density plots, especially in plots with higher water motion (treatment effect,  $p < 0.0001$ ; mass transfer by treatment interaction,  $p < 0.0001$ ).

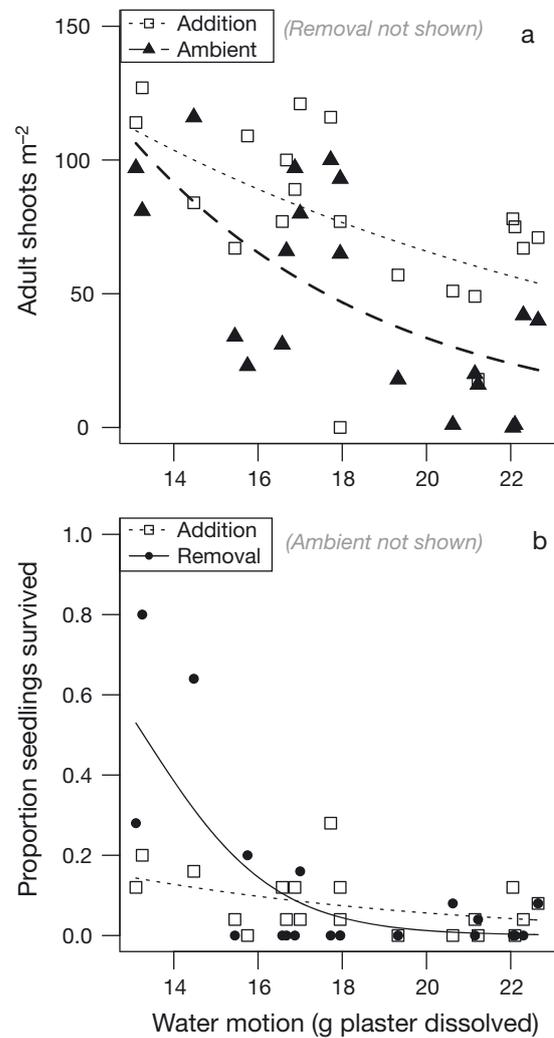


Fig. 3. Eelgrass (*Zostera marina*) survival along the increasing hydrodynamic gradient, as measured by increasing water motion. (a) Adult shoot density counts at the end of the experiment for unmanipulated shoot density (ambient) and addition treatments (removal treatment data not shown because all counts were 0 shoots  $m^{-2}$ ). (b) Proportion of the 25 transplanted seedlings that survived to the end of the experiment (end of July) in addition (120 adult shoots  $m^{-2}$ ) and removal (0 shoots  $m^{-2}$ ) treatments (ambient plots contained intermediate, non-constant vegetative shoot density, and thus were not compared)

### Effect of adult eelgrass canopy on seedling survival

Seedling survival overall was higher at the 'calm' end of the hydrodynamic gradient (binomial GLM,  $p < 0.0001$ ). Seedling survival was influenced by 'addition' versus 'removal' of adult eelgrass, but effects depended on water motion (treatment by water motion interaction: end of July,  $p < 0.0001$ ) (Fig. 3b). Specifically, the presence of adult eelgrass shoots (120 shoots

$m^{-2}$ ) increased survival where water motion was high, and decreased survival where water motion was low. The transition between positive and negative effects for the final time point (end of July) occurred at 16.9 g plaster dissolved (Fig. 3b). Thus, adding adult eelgrass shoots had a positive effect on seedling survival in plots with higher water motion but actually had a negative effect on seedling survival in plots experiencing less water motion. It is important to note that any positive effect due to adult eelgrass engineering in the more exposed plots would be conservative since the shoot density in the 'addition' treatments was allowed to return towards ambient density over the course of the experiment (see 'Adult eelgrass density manipulation' results above, Fig. 3a).

### Effect of adult eelgrass canopy on seedling morphology

Treatments with adult eelgrass present (ambient and addition treatments) had a significant effect on final seedling length (LRT,  $p < 0.0001$ ), seedling width (LRT,  $p < 0.0001$ ), and number of branches (LRT,  $p = 0.001$ ). However, water motion did not affect any of these seedling morphological traits, nor was there an eelgrass treatment by water motion interaction. Seedlings in the removal plots had larger shoots with higher rates of branching compared to addition and ambient plots (Fig. 4a–c). The number of rhizome internodes was affected by neither eelgrass treatment nor water motion (Fig. 4d).

### DISCUSSION

Overall, our results support the stress gradient hypothesis for eelgrass, a marine ecosystem engineer, along a gradient of water motion (i.e. stress). Although the physical engineering effects of eelgrass were to decrease water motion consistently, the direction of intraspecific interactions of eelgrass reversed along a spatial gradient in water flow. Specifically, greater water motion was stressful for eelgrass adults and seedlings, decreasing their survival (Fig. 3). In conditions of greater water motion, the presence of adult eelgrass ( $120 \text{ shoots } m^{-2}$ ) was there-

fore associated with relatively higher seedling survival than in plots with all adult eelgrass removed ( $0 \text{ shoots } m^{-2}$ ) (Fig. 3). Supporting the stress gradient hypothesis, the positive impact of ecosystem engineering by eelgrass disappeared in calmer hydrodynamic conditions, where a high density of adult shoots negatively impacted seedling survival (Fig. 3). Presumably, this was due to competition for light or other resources, as evidenced by the uniformly smaller size of seedlings in the treatments with eelgrass present (ambient and addition plots, Fig. 4), although these environmental variables were not quantified in this experiment. Thus, eelgrass was not always a facilitative ecosystem engineer; in less stressful environments, the impacts of negative, intra-specific interactions exceeded that of facilitative interactions via the abiotic environment. These results are consistent with community-level impacts of structure-forming plants in benign conditions of other systems, both aquatic (e.g. Crain & Bertness 2005, Daleo & Iribarne 2009, He et al. 2011) and terrestrial (e.g. Choler et al. 2001).

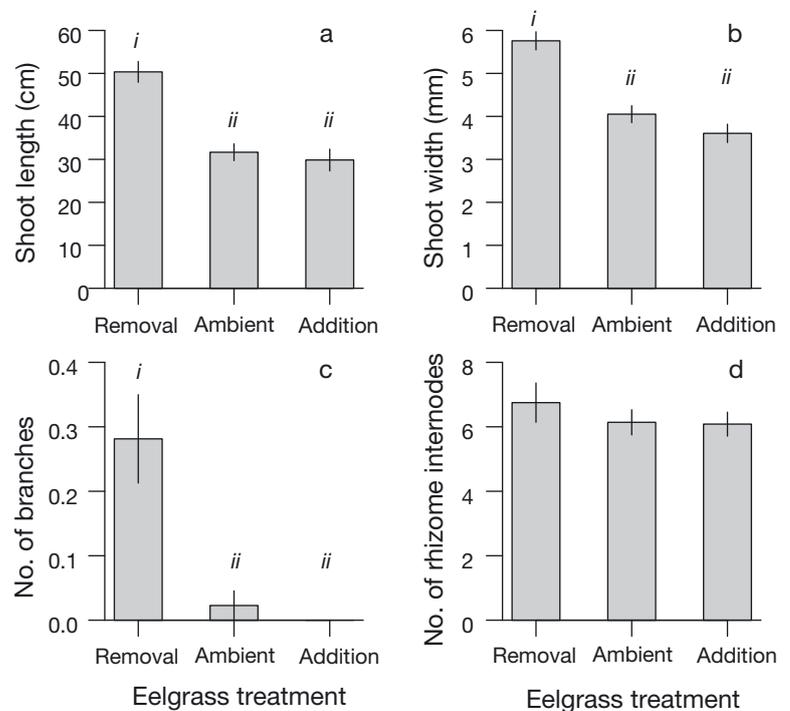


Fig. 4. *Zostera marina*. Although adding an adult canopy facilitated seedling survival in exposed conditions, adult-seedling competition was present regardless of hydrodynamic context, as evidenced by seedling morphometrics: (a) mean shoot length, (b) mean shoot width, (c) mean number of branches, and (d) mean number of rhizome internodes of all seedlings in each plot. Bars depict standard error amongst the means of the metric for all seedlings in each of the plots in the particular treatment. Different roman numerals indicate significant differences ( $p < 0.05$ )

Understanding the mechanism by which eelgrass modifies the physical environment provides an explanation for the reversal of intraspecific effects we observed. 'Autogenic engineers' (Jones et al. 1994) modify the environment as passive physical structures, for example, by impeding fluid flow (e.g. barnacles: Bertness 1989; sea palm algae: Holbrook et al. 1991; terrestrial crops: Finnigan 2000), with potentially sizeable impacts when in large numbers (Power et al. 1996). As an autogenic engineer, eelgrass provided physical structure and flow amelioration regardless of the overlying context of water motion (Fig. 2). However, the implications of engineering for facilitating eelgrass depended on other intraspecific interactions. Competitive interactions dominated at low water motion and presumably outweighed the facilitative impacts of eelgrass, resulting in context-dependent engineering. Thus, the present study emphasizes the value of empirically measuring and comparing the overlying abiotic context and the modification provided by the engineer (as per Jones & Gutierrez 2007), as well as the direct biotic interactions influencing the engineer (theoretically modeled by Cuddington & Hastings 2004). This is especially so for autogenic engineers, for which the strength of engineering will be of relative magnitude compared to the strength of intraspecific interactions. This supports theoretical expectations that colonization by an ecosystem engineer that makes the habitat more suitable for itself will initially be slow in suboptimal habitats, until habitat modification becomes sufficient for population persistence (Olesen & Sand-Jensen 1994, Cuddington & Hastings 2004).

High hydrodynamic energy may ultimately limit the carrying capacity of eelgrass (e.g. Fonseca & Bell 1998), but our results also imply that eelgrass itself can increase its own densities under certain environmental conditions, potentially leading to rapid recovery following disturbance. Examples of eelgrass beds that have recovered rapidly (<1 yr) by seed and seedlings appear to be in shallow embayments where the stressor was temporary, and there was whole meadow mortality (e.g. Plus et al. 2003, Lee et al. 2007). In these estuaries, wave energy may be relatively lower, due to shallow water depth. Presumably, environmental features, such as calmer hydrodynamic conditions and lack of intraspecific interactions with adult shoots, allowed for seed retention, germination, and initial seedling survival in the first year of the study by Lee et al. (2007). One study in a Danish estuary also reported rapid recolonization by seedlings, following a dieback event that did not lead to full-bed mortality (4% of shoots survived the

dieback event; Greve et al. 2005). While contributing via asexual reproduction, the very low density of adult shoots and the remaining rhizome network may have stabilized the sediment and reduced tidal currents (Greve et al. 2005) to facilitate seed and seedling retention. In contrast, other studies demonstrate much longer recovery times (12 yr), requiring seed addition by humans (McGlathery et al. 2012, Orth et al. 2012). At higher levels of hydrodynamic exposure, seedlings generally cannot survive and instead erode away (Koch et al. 2010, Valdemarsen et al. 2010), possibly leaving an area unvegetated for a long period. Further study is necessary to determine whether overlying hydrodynamic factors relative to surviving eelgrass shoot density could have led to variable recovery speeds and trajectories of each of these embayments, as opposed to other abiotic and biotic factors (e.g. Valdemarsen et al. 2011).

Potentially, the very mechanism that can lead to sudden declines of eelgrass meadows and seemingly prevent natural regeneration also provides a solution for restoration ecologists. At hydrodynamically exposed sites, where facilitative interactions likely played a role in maintaining original eelgrass beds and natural regeneration is delayed, human actions may tip the balance towards restoration (Suding et al. 2004). Specifically, recovery of self-maintaining seagrass meadows may be achieved by creating temporary protective structures or restoring a sparse adult canopy while adding seed—a strategy that is resource-intensive in the short term, but self-maintaining in the long term. This fits with observations in other marine systems. For example, restoration of a reef-building oyster in a long-term decline was only successful when oysters were planted at high densities, facilitating juvenile recruitment (Schulte et al. 2009). The possibility of sudden and persistent declines by eelgrass and other autogenic engineers emphasizes explicit quantification of habitat modification by the engineer relative to its environmental context. More generally, the stress gradient hypothesis can provide an important framework for conservation and restoration practitioners hoping to understand the contexts under which imperiled and important ecosystem engineers decline precipitously and facilitate their own recovery (e.g. eelgrass, cordgrass, oysters, corals) (Byers et al. 2006).

*Acknowledgements.* We thank E. Fuller for field assistance and B. Kemmer and Taylor Shellfish Farms for tidelands access. This study was supported by fellowships from the Environmental Protection Agency Science to Achieve Results Program, Achievement Rewards for College Scientists, and the National Science Foundation GK-12 Ocean

and Coastal Interdisciplinary Science Program (to S.Y.). Thanks to 3 anonymous reviewers, this manuscript was greatly improved.

#### LITERATURE CITED

- Baden SP, Boström C (2001) The leaf canopy of seagrass beds: faunal community structure and function in a salinity gradient along the Swedish coast. In: Reise K (ed) Ecological comparisons of sedimentary shores. *Ecol Stud* 151:213–236
- Banas NS, Hickey BM, MacCready P, Newton JA (2004) Dynamics of Willapa Bay, Washington: a highly unsteady, partially mixed estuary. *J Phys Oceanogr* 34: 2413–2427
- Bertness MD (1989) Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* 70: 257–268
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18: 119–125
- Byers J, Cuddington K, Jones C, Talley T and others (2006) Using ecosystem engineers to restore ecological systems. *Trends Ecol Evol* 21:493–500
- Callaway RM (1992) Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73:2118–2128
- Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308
- Crain CM, Bertness MD (2005) Community impacts of a tussock sedge: Is ecosystem engineering important in benign habitats? *Ecology* 86:2695–2704
- Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* 56:211–218
- Cuddington K, Hastings A (2004) Invasive engineers. *Ecol Model* 178:335–347
- Cuddington K, Wilson W, Hastings A (2009) Ecosystem engineers: feedback and population dynamics. *Am Nat* 173:488–498
- Daleo P, Iribarne O (2009) Beyond competition: the stress-gradient hypothesis tested in plant-herbivore interactions. *Ecology* 90:2368–2374
- Finnigan J (2000) Turbulence in plant canopies. *Annu Rev Fluid Mech* 32:519–571
- Fonseca MS, Bell SS (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar Ecol Prog Ser* 171:109–121
- Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Program Decision Analysis Series No. 12. NOAA Coastal Ocean Office, Silver Spring, MD
- Gaeckle J, Dowty P, Berry H, Ferrier L (2011) Puget Sound submerged vegetation monitoring project 2009 monitoring report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, WA
- Green D, Crowe T (2014) Context- and density-dependent effects of introduced oysters on biodiversity. *Biol Invasions* 16:1145–1163
- Greve TM, Krause-Jensen D, Rasmussen MB, Christensen PB (2005) Means of rapid eelgrass (*Zostera marina* L.) recolonisation in former dieback areas. *Aquat Bot* 82:143–156
- He Q, Cui B, An Y (2011) The importance of facilitation in the zonation of shrubs along a coastal salinity gradient. *J Veg Sci* 22:828–836
- He Q, Bertness MD, Altieri AH (2013) Global shifts toward positive species interactions with increasing environmental stress. *Ecol Lett* 16:695–706
- Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. *Mar Ecol Prog Ser* 253:123–136
- Holbrook NM, Denny MW, Koehl MAR (1991) Intertidal tree—consequences of aggregation on the mechanical and photosynthetic properties of sea-palms *Postelsia palmaeformis* Ruprect. *J Exp Mar Biol Ecol* 146:39–67
- Jones CG, Gutierrez JL (2007) On the purpose, meaning, and usage of the physical ecosystem engineering concept. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: plants to protists. Theoretical Ecology Series. Academic Press, Burlington, MA, p 3–24
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957
- Koch EW, Ackerman JD, Verduin J, van Keulen M (2006) Fluid dynamics in seagrass ecology—from molecules to ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, p 193–225
- Koch EW, Ailstock MS, Booth DM, Shafer DJ, Magoun AD (2010) The role of currents and waves in the dispersal of submersed angiosperm seeds and seedlings. *Restor Ecol* 18:584–595
- Lambrinos JG (2007) Managing invasive ecosystem engineers: the case of *Spartina* in Pacific estuaries. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: plants to protists. Theoretical Ecology Series. Academic Press, Burlington, MA, p 299–322
- Lee K, Park J, Kim YK, Park SR, Kim J (2007) Recolonization of *Zostera marina* following destruction caused by a red tide algal bloom: the role of new shoot recruitment from seed banks. *Mar Ecol Prog Ser* 342:105–115
- Marion SR, Orth RJ (2010) Factors influencing seedling establishment rates in *Zostera marina* and their implications for seagrass restoration. *Restor Ecol* 18: 549–559
- McGlathery KJ, Reynolds LK, Cole LW, Orth RJ, Marion SR, Schwarzschild A (2012) Recovery trajectories during state change from bare sediment to eelgrass dominance. *Mar Ecol Prog Ser* 448:209–221
- Molinari N, D'Antonio C, Thomson G (2007) *Carpobrotus* as a case study of the complexities of species impacts. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: plants to protists. Theoretical Ecology Series. Academic Press, Burlington, MA, p 150–151
- Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution. Princeton University Press, Princeton, NJ
- Olesen B, Sand-Jensen K (1994) Patch dynamics of *Zostera marina*. *Mar Ecol Prog Ser* 106:147–156
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. *Bioscience* 56:987–996

- Orth RJ, Moore KA, Marion SR, Wilcox DJ, Parrish DB (2012) Seed addition facilitates eelgrass recovery in a coastal bay system. *Mar Ecol Prog Ser* 448:177–195
- Plus M, Deslous-Paoli J, Dagault F (2003) Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquat Bot* 77:121–134
- Porter ET, Sanford LP, Suttles SE (2000) Gypsum dissolution is not a universal integrator of 'water motion'. *Limnol Oceanogr* 45:145–158
- Power ME, Tilman D, Estes JA, Menge BA and others (1996) Challenges in the quest for keystones. *Bioscience* 46: 609–620
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.R-project.org](http://www.R-project.org)
- Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325:1124–1128
- Scyphers SB, Powers SP (2013) Context-dependent effects of a marine ecosystem engineer on predator–prey interactions. *Mar Ecol Prog Ser* 491:295–301
- Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. *Environ Conserv* 23:17–27
- Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* 19:46–53
- Thompson TL, Glenn EP (1994) Plaster standards to measure water motion. *Limnol Oceanogr* 39:1768–1779
- Valdemarsen T, Canal-Vergés P, Kristensen E, Holmer M, Kristiansen MD, Flindt MR (2010) Vulnerability of *Zostera marina* seedlings to physical stress. *Mar Ecol Prog Ser* 418:119–130
- Valdemarsen T, Wendelboe K, Egelund JT, Kristensen E, Flindt MR (2011) Burial of seeds and seedlings by the lugworm *Arenicola marina* hampers eelgrass (*Zostera marina*) recovery. *J Exp Mar Biol Ecol* 410:45–52
- van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. *Ecosystems* 10: 1311–1322

Editorial responsibility: Kenneth Heck Jr.,  
Dauphin Island, Alabama, USA

Submitted: July 23, 2014; Accepted: November 19, 2015  
Proofs received from author(s): January 17, 2016