THE LIVING SHORELINE APPROACH AS AN ALTERNATIVE TO SHORELINE HARDENING: IMPLICATIONS FOR THE ECOLOGY AND ECOSYSTEM SERVICE DELIVERY OF SALT MARSHES

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ABSTRACT

Rachel K. Gittman: The Living Shoreline Approach as an Alternative to Shoreline Hardening: Implications for the Ecology and Ecosystem Service Delivery of Salt Marshes (Under the direction of John F. Bruno and Charles H. Peterson)

Foundation species, such as marsh plants, mangroves, seagrasses, corals, and oysters, form some of the most valuable and threatened habitats in the world. The loss of these coastal habitat-forming species often results in significant changes in community structure and ecosystem-service delivery. Therefore, understanding how both biotic (e.g., herbivory) and abiotic (e.g., drought) factors can alter foundation species' structure is critical for promoting resilience to anthropogenic stressors. My dissertation focused on how physical and biological processes regulate salt marshes, and how coastal development, specifically shoreline hardening, affects two marsh ecosystem services: erosion protection and habitat provision for marine fauna. Marsh cordgrass (Spartina alterniflora) is a highly productive foundation species that can inhibit coastal erosion. However, anoxic stress can allow marsh periwinkles to overgraze marshes, resulting in marsh die-off. Burrowing crabs can alleviate anoxic stress (via sediment bioturbation) and thus can potentially sustain marsh productivity. From field experiments (Ch.1), I found that crab bioturbation allowed Spartina to compensate for biomass losses from periwinkle grazing. Unfortunately, shoreline hardening (construction of bulkhead or riprap structures) can reduce marsh access for burrowing crabs and thus increase sediment anoxia, preventing marshes from keeping pace with overgrazing. In Ch. 2, I quantified the prevalence of shoreline hardening in the United States and found that 14% of the shoreline is hardened.

Housing density is positively correlated with hardening along the Atlantic, Pacific, and Gulf sheltered coasts. With projected accelerated population growth along U.S. coasts, marshes may be lost to future shoreline hardening. Heightened awareness of adverse effects of shoreline hardening has increased demand for "living shorelines". Living shorelines include marsh plantings with or without offshore sills. My field surveys of different shoreline types show that living shorelines provide superior erosion protection to bulkheads during a Category 1 hurricane (Ch. 3). Further, by sampling marine fauna in hardened and living shoreline habitats, I show that living shorelines provide better habitat for fish and crustaceans than hardened shorelines lacking marsh (Ch. 4). Therefore, although shoreline hardening is still commonly used for erosion protection, marshes may prevent erosion better than bulkheads during storm events, while also serving as valuable habitat.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
BACI	Before-after-control-impact
CI	Control-impact
GPS	Global positioning system
MSL	Mean sea level
NAVD88	North American Vertical Datum of 1988
OHWM	Observed high water mark
SOM	Sediment organic matter

CHAPTER 1: FIDDLER CRABS FACILITATE SPARTINA ALTERNIFLORA GROWTH, MITIGATING PERIWINKLE OVERGRAZING OF MARSH HABITAT¹

Abstract

Ecologists have long been interested in identifying and testing factors that drive top-down or bottom-up regulation of communities. Most studies have focused on factors that directly exert top-down (e.g., grazing) or bottom-up (e.g., nutrient availability) control on primary production. For example, recent studies in salt marshes have demonstrated that fronts of Littoraria irrorata periwinkles can overgraze Spartina alterniflora and convert marsh to mudflat. The importance of indirect, bottom-up effects, particularly facilitation, in enhancing primary production has also recently been explored. Previous field studies separately revealed that fiddler crabs, which burrow to depths of more than 30 cm, can oxygenate marsh sediments and redistribute nutrients, thereby relieving the stress of anoxia and enhancing S. alterniflora growth. However, to our knowledge, no studies to date have explored how non-trophic facilitators can mediate top-down effects (i.e., grazing) on primary producer biomass. We conducted a field study testing whether fiddler crabs can facilitate S. alterniflora growth sufficiently to mitigate overgrazing by periwinkles and thus sustain S. alterniflora marsh. As inferred from contrasts to experimental plots lacking periwinkles and fiddlers crabs, periwinkles alone exerted top-down control of total above-ground biomass and net growth of S. alterniflora. When fiddler crabs were included, they counteracted the effects of periwinkles on net S. alterniflora growth. Sediment oxygen levels

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were greater and *S. alterniflora* below-ground biomass was lower where fiddler crabs were present, implying that fiddler crab burrowing enhanced *S. alterniflora* growth. Consequently, in the stressful interior *S. alterniflora* marsh, where subsurface soil anoxia is widespread, fiddler crab facilitation can mitigate top-down control by periwinkles and can limit and possibly prevent loss of biogenically-structured marsh habitat and its ecosystem services.

Introduction

Community structure and function are regulated by both the availability of resources (bottom-up) and by consumption (top-down) (e.g., Hairston et al. 1960, White 1978). For decades, ecologists have debated the relative importance of top-down versus bottom-up forces (Fretwell 1977, Power 1992, Strong 1992). Recent reviews indicate that the debate has expanded beyond whether communities are top-down or bottom-up controlled to incorporate additional factors, such as differences between terrestrial and aquatic ecosystems, variation in producer traits, and the effects of environmental heterogeneity (Worm et al. 2002, Shurin et al. 2006, Burkepile and Hay 2006, Gruner et al. 2008, Poore et al. 2012).

Environmental heterogeneity (i.e., variation in abiotic factors) is predicted to affect the relative strength of top-down and bottom-up forces (Hunter and Price 1992), and studies within the past decade have begun to experimentally test hypotheses resulting from this prediction (Moon and Stiling 2000, Menge et al. 2002, Alberti et al. 2009, Shurin et al. 2012). For example, Shurin et al. (2012) provided evidence for higher temperatures promoting stronger top-down control of an aquatic food web via warming-induced reductions in producer biomass without concomitant reductions in zooplankton, zoobenthos, and pelagic bacteria biomass. In addition, Moon and Stiling (2002) showed that increased salinity resulted in stronger bottom-up control of

a salt marsh plant-parasite-parasitoid system because increases in salinity increased the number of galls (containing larvae) on *Borrichia fructescens* stems, while simultaneously decreasing parasitism of galls. In a thorn scrub community in north-central Chile, high rainfall events caused by periodic El Niño Southern Oscillation (ENSO) events shifted community regulation from topdown to bottom-up through increases in primary production. Whether a community is top-down or bottom-up regulated appears to depend on which trophic level (e.g., producer, herbivore) is most affected by the changing abiotic factor (e.g., temperature, salinity). Both the internal stress tolerances of affected organisms (e.g., Alberti et al. 2009) and external stress amelioration by cooccurring organisms (Bruno et al. 2003) could thus determine the direction of control.

Non-trophic facilitation (i.e., facilitation by an organism that is not a predator or prey to the organisms regulating primary producer biomass) has largely been ignored as a factor that could affect the direction or magnitude of ecosystem or community regulation. The model developed by Menge and Sutherland (1976) and modified by Bruno et al. (2003) predicts that under moderate to high stress levels and with high basal species (e.g., primary producer) recruitment, stress amelioration (bottom-up) may play a larger role in regulating basal species abundance (or biomass) than consumptive (top-down) forces. If stress is alleviated, resultant higher rates of production would likely outpace biomass losses to grazing. Although more recent studies have shown that facilitation can have strong, bottom-up affects on community structure (Altieri et al. 2007, 2010), no studies to our knowledge have experimentally tested the hypothesis that stress amelioration by non-trophic facilitators allows a species to compensate for losses to consumption. In this study, we propose to test the hypothesis that non-trophic facilitation can change the magnitude and/or direction of regulation of a primary producer.

We selected the salt marsh as our study system for testing this hypothesis because rigorous field experiments have provided experimental evidence for both bottom-up (Morris 1982, Moon and Stiling 2002) and top-down (Silliman and Zieman 2001, Silliman and Bertness 2002, Silliman et al. 2005) regulation of primary producer standing biomass and production. Salt marshes are generally categorized as moderate-to-high-stress environments for vascular plants as a result of high salinity and anoxia in the sediments (Bertness and Ellison 1987). S. alterniflora, marsh cordgrass, is a foundation (habitat-forming) species (Dayton 1972) well adapted to this environment; however, S. alterniflora production can be limited by both environmental stress and nutrient availability (Emery et al. 2001). Silliman and Zieman (2001) showed that the marsh periwinkle (*Littoraria irrorata*), a common marsh resident, can exert strong top-down control on S. alterniflora when in sufficient densities. Additionally, scarring and fungal-farming by high densities of marsh periwinkles can increase the rate of a drought-induced marsh die-off (Silliman and Newell 2003, Silliman et al. 2005). In contrast, the fiddler crabs, Uca pugnax and Uca *pugilator*, are bioturbators that oxygenate sediments and actively transport nutrients (e.g., nitrogen) and organic matter through the marsh sediment layers, which subsequently facilitates salt marsh (S. alterniflora) production (Bertness 1985, McCraith et al. 2003, Daleo et al. 2007, Angelini and Silliman 2012). However, it is unclear whether facilitation of S. alterniflora production by fiddler crabs could reduce the magnitude of top-down control by marsh periwinkles. Therefore, we hypothesized that facilitation via fiddler crab bioturbation (amelioration of low oxygen stress) and/or nutrient redistribution (enhancement of resource availability) will mediate overgrazing on S. alterniflora.

Methods

Description of Study Site

We conducted our field experiment within a salt marsh at Hoop Pole Creek Clean Water Reserve in Atlantic Beach, NC (34°42'25.12"N, 76°45'1.14"W) and our field surveys at Hoop Pole Creek and the Theodore Roosevelt Natural Area in Pine Knoll Shores (PKS), NC (34°42'1.12"N, 76°49'57.50"W). Hoop Pole Creek is characterized by a 70 m by 50 m peninsula dominated by *S. alterniflora* in the low to intermediate marsh zones and by *Juncus roemerianus* in the high marsh zone. Other common plant species found throughout the high marsh include *Spartina patens, Salicornia virginica, Distichlis spicata, Borrichia fructescens*, and *Limonium carolinium*. We conducted our study in the intermediate marsh zone, where short-form *S. alterniflora* dominates because environmental stressors, such as sediment anoxia and salinity, are typically highest within this zone of the marsh (Bertness and Ellison 1987). Marsh periwinkles and fiddler crab burrows are both most abundant in this zone of the marsh (R.K. Gittman, *unpublished data*). We expected marsh periwinkle grazing and fiddler crab bioturbation and nutrient deposition to have the greatest effect on *S. alterniflora* standing biomass and production in this zone because *S. alterniflora* growth is most limited by environmental stress here.

Field experimental design and setup

We experimentally manipulated the density of fiddler crabs and marsh periwinkles at Hoop Pole Creek marsh in June 2011 to test the hypothesis that fiddler crab bioturbation can facilitate *S. alterniflora* growth, thus mitigating the effects of marsh periwinkle grazing on *S. alterniflora*. Within the short-form *S. alterniflora* zone (approximately 3,500 m²), we established 30, one m by one m plots, minimizing differences in elevation, sediment type, and *S. alterniflora* density. Each plot was assigned one of the following treatments (n=6) in a stratified random

design: (1) fiddler crab removal and marsh periwinkle addition; (2) periwinkle removal and fiddler crab addition; (3) fiddler crab and periwinkle removal; (4) fiddler crab and periwinkle addition; and (5) open (unmanipulated, ambient fiddler crab and periwinkle densities).

To prevent fiddler crabs and periwinkles from entering or exiting plots after establishing and recording initial densities, we installed five mm hardware cloth enclosures 15 cm into the ground around each plot and lined the top of the enclosure with aluminum flashing (Silliman and Zieman 2001, Holdredge et al. 2010). Open plots with no enclosures or faunal manipulations were established to represent ambient conditions. We walked the perimeter of open plots to mimic the disturbance associated with the installation of the cages and also took light measurements (photosynthetically active radiation (PAR)) inside and outside of the enclosures to ensure that there were no shading effects (Appendix 1.A). Prior to the start of the experiment, we removed all marsh periwinkles and fiddler crabs from the surface and collapsed visible burrows in the plots daily for ten days for all treatments except the open, ambient density treatment. We then added 300 individually labeled marsh periwinkles with a wet weight of 1.58±0.14 g and shell length of 18.65±0.59 mm per individual to each periwinkle addition plot, and added 75 labeled fiddler crabs (50 U. pugilator and 25 U. pugnax to match field density ratios found within the marsh) with a wet weight of 1.22 ± 0.08 g and carapace width of 14.48 ± 0.19 mm per individual, to each fiddler crab addition plot. We verified the presence of labeled fiddler crabs and periwinkles in addition plots and removed periwinkles and fiddler crabs from the surface of the sediment in removal plots weekly throughout the experiment (Appendix 1.A). The experiment was concluded at the landfall of Hurricane Irene on 27 August 2011 because damage to enclosure necessarily ended the experiment (Figure 1.A1). At the conclusion of the experiment, we counted fiddler crab burrows in treatment plots and we collected, measured and

weighed (dry tissue and shell mass, grams) all labeled periwinkles from each plot (Appendix 1.A). To determine periwinkle-grazing intensity, we measured the length of each leaf and of periwinkle radulation scars per *S. alterniflora* stem clipped at the base from the center 0.0625-m² section of the plot.

S. alterniflora standing biomass and production

We quantified the stem density and measured the height of the tallest live leaf of each *S. alterniflora* plant within 0.0625-m² areas at the center of each one-m² plot at the beginning, midpoint, and end of the experiment to minimize enclosure boundary effects on *S. alterniflora*. We used the difference in summed live leaf heights of all live plants from the beginning to the end of the experiment to estimate *S. alterniflora* net growth during the experiment. At the conclusion of the experiment, we clipped, measured, and dried (at 60°C for two weeks) all *S. alterniflora* stems (live and dead) at their base within the center 0.0625-m² area within each plot to determine the standing crop (g dry mass/m²). We then took two, 7.5-cm diameter, 30-cm deep cores within the 0.0625-m² center of each plot to determine below-ground biomass. *S. alterniflora* roots and rhizomes are typically concentrated within the top 25 cm of sediment (Howes et al. 1981). Therefore, samples are representative of total below-ground biomass. Cores were divided into 5-cm thick sections, sieved (2-mm mesh), then sorted into roots and rhizomes or other plant material, dried at 60°C for two weeks, and weighed following the methods of Bertness (1985). *S. alterniflora tissue nitrogen concentration*

Because fiddler crabs can increase the supply of nitrogen available to marsh plants through bioturbation and biodeposition, and because marsh periwinkle grazing requires *S*. *alterniflora* plants to allocate resources to replace leaf tissue, we measured the carbon content (% C), nitrogen content (% N), and carbon to nitrogen ratio (C:N) by clipping, drying, grinding, and

acidifying (to remove inorganic nitrogen), and analyzing a section of the youngest shoot of each of ten harvested *S. alterniflora* using a Perkin Elmer Series II 2400 CHNS/O Analyzer. *Sediment redox potential*

To determine effects of fiddler crab bioturbation on the marsh sediment oxygen availability, we measured sediment redox potential (mV) within each plot. *In situ* redox measurements were made using a bare platinum electrode probe and a Fisher Scientific Accumet double junction Ag/AgCl electrode (+200 mV correction added to the measured value), connected through a Fisher Scientific Accumet pH/mV/ °C meter, model AP71. Electrodes were placed 10 cm into the sediment and left over one tidal cycle before readings were taken to allow the sediment around the probe to stabilize. We measured redox potential immediately after cage installation on June 14th (prior to removals or additions), June 24th, July 26th and August 30th. *Field surveys*

To determine the density and distribution of *S. alterniflora* within continuous short-form *S. alterniflora* region and within nearby short-form *S. alterniflora* die-off front (covering approximately 1,000-1,500 m²) at our study site, we sampled *S. alterniflora* stem density per 0.25-m² within ten randomly placed quadrats. We defined the short-form *S. alterniflora* region as being greater than 20 m from the marsh edge, dominated by short-form *S. alterniflora* (95 to 100% cover), and at least 20 m from any visible die-off front. Die-off fronts were defined as short-form *S. alterniflora* regions directly adjacent to unvegetated areas in the upper to intermediate marsh zone. We sampled the density of fiddler crab burrows and marsh periwinkles and took sediment redox (mV) measurements. To determine if patterns observed were unique to our study site, we repeated this sampling protocol at a salt marsh with a die-off front of similar

size and with similar shoreline orientation and tidal patterns within the Theodore Roosevelt Natural Area in PKS, NC, located 100 m southwest of the PKS Aquarium pier.

Statistical Analysis

We compared periwinkle and fiddler crab addition and removal effects on the following response variables using separate one-way analyses of variance (ANOVAs): S. alterniflora above-ground and below-ground biomass, the mean proportion of scarred (via periwinkle radulations) to total live leaf length (cm), the difference in stem density and in live summed stem heights between the beginning and end of the experiment, S. alterniflora C (%), N (%), and C:N. Differences between specific sets of treatments (e.g., periwinkle addition treatments to periwinkle removal treatments, pooled across fiddler crab treatments) were assessed using a priori planned comparisons. The mean proportion of scarred to live leaf length was arcsine square root transformed prior to analysis to meet the assumptions of ANOVA. To verify the effectiveness of fiddler crab and periwinkle density manipulations during the experiment, we used one-way ANOVAs to compare the final marsh periwinkle counts, shell growth, weight change, and body mass proportions, and fiddler crab burrow counts, across pooled removal and addition treatments (Appendix 1.A). We compared sediment redox potential between treatments and through time using repeated-measures ANOVA, and compared treatments at each time using one-way ANOVAs and planned comparisons. We compared survey data (live and dead S. alterniflora stem density, stem height, fiddler crab burrow density, marsh periwinkle density, and sediment redox potential) across marsh type (intermediate marsh zone vs. die-off front) using one-way ANOVAs for each site. Because we applied each statistical test to separate, pre-defined hypotheses, we made no corrections to alpha values for this study (Hurlbert and Lombardi 2003, Moran 2003). All analyses were performed using JMP software version 9.0 (SAS Institute 2010).

Results

Field Experiment

S. alterniflora response-The mean change in S. alterniflora stem density from the beginning to the end of the experiment did not differ between periwinkle addition and periwinkle removal treatments, nor did stem density differ between fiddler crab addition and removal treatments (Fig. 1.1 A, P = 0.36 and P = 0.76, respectively, Table 1.C1). S. alterniflora aboveground biomass was significantly reduced in periwinkle addition treatments when compared to periwinkle removal treatments, but did not differ between fiddler crab addition and fiddler crab removal treatments (Fig. 1.1B, P = 0.043 and P = 0.64, respectively, Table 1.C2). The proportion of scarred to intact live leaf tissue was greater in periwinkle addition treatments than periwinkle removal treatments (Fig. 1.1C, P < 0.001, Table 1.C3). Fiddler crab presence or absence did not affect the amount of scarred leaf tissue in periwinkle addition treatments (P = 0.89, Table 1.C3). S. alterniflora summed live stem heights (cm), used as a proxy for net S. alterniflora growth, increased in fiddler crab addition, fiddler crab and periwinkle addition, and fiddler crab and periwinkle removal treatments, but decreased in the periwinkle addition and fiddler crab removal treatment (Fig. 2, P = 0.01, Table 1.C4). However, there was no difference in the change in live stem height between the fiddler crab addition and periwinkle removal treatment and the fiddler crab and periwinkle removal treatment (P = 0.54, Table 1.C4). N (%), C (%), and C:N in new S. *alterniflora* shoots did not differ among treatments (Tables 1.B1-5, P > 0.05). Fiddler crab addition plots had lower total below-ground biomass (0-25 cm depth) than fiddler crab removal plots, regardless of the periwinkle treatment (Fig. 1.3A, P = 0.026, Table 1.C5). Below-ground

biomass decreased with depth for all treatments, with the largest difference between fiddler crab addition and fiddler crab removal plots being at a depth of 10-15cm (Fig. 1.3B).

Sediment redox potential- Marsh sediment redox potential (mV) decreased from initial values measured on June 14th (pre-addition or removal) in fiddler crab removal plots to values measured on June 24th, and then returned to initial redox values in July and August (Fig. 1.3C, *see* Tables 1.D1-5 for statistical analysis results). In contrast to the fiddler crab removal plots, redox in fiddler crab addition and open plots did not decrease in June, however; all enclosure treatments had lower redox than open plots immediately after enclosure installation (Fig. 1.3C, Table 1.D1-5).

Field surveys

The density of live *S. alterniflora* stems did not differ between the continuous marsh regions and along die-off fronts at either our experimental study site or at the PKS marsh (P = 0.726 and P = 0.121, respectively, Tables 1.1, 1.E1-2). The maximum live stem height was greater in the continuous marsh than along the die-off fronts at both sites (P < 0.001 and P = 0.01, respectively, Tables 1.1, 1.E1-2). Standing dead stem density was greater in the die-off fronts at both sites than in the continuous marsh (P = 0.047 and P < 0.001, respectively, Tables 1.1, 1.E1-2). Marsh periwinkle density did not differ between the continuous marsh and die-off fronts (P = 0.246 and P = 0.898, respectively, Tables 1.1, 1.E1-2). Fiddler crab burrow density was higher in the continuous marsh than in the die-off fronts at both sites (P < 0.0001 and P = 0.019, respectively, Tables 1.1, 1.E1-2). Sediment redox potential did not differ between continuous marsh and the die-off fronts at either site (P = 0.833 and P = 0.160, respectively, Tables 1.1, 1.E1-2).

Discussion

Facilitation mitigates top-down control of S. alterniflora

Our results suggest that periwinkle scarring and grazing can decrease total above-ground biomass of S. alterniflora (Fig. 1.1B-C), which is consistent with, but less pronounced than the results of previous research (Silliman and Zieman 2001, Silliman and Bertness 2002). However, total above-ground biomass includes both live and dead leaf tissue from live S. alterniflora plants. Therefore, we measured live stem height to determine whether fiddler crabs, through bioturbation or biodeposition, could facilitate new, compensatory growth of grazed S. alterniflora plants. Net S. alterniflora growth in plots with high densities of fiddler crabs and marsh periwinkles was positive and equivalent to growth in plots where both organisms were removed, but net growth was negative when just high densities of periwinkles were present (Fig. 1.2). Because there was no difference in scarring between periwinkle treatments with and without fiddler crabs, we can conclude that fiddler crabs did not affect periwinkle grazing, but instead facilitated compensatory growth of S. alterniflora in response to periwinkle grazing. We acknowledge that initiating the experiment in June, two months after the start of the S. alterniflora growing season, likely underestimates the effects of periwinkle grazing on S. alterniflora. However, the effects of fiddler crab stress amelioration via bioturbation on S. alterniflora is also likely to be underestimated because fiddler crabs become active in March in North Carolina (Colby and Fonseca 1984). Therefore, the relative strength of the effects of periwinkles and fiddler crabs are not likely to change with the timing of the experiment.

Net growth of *S. alterniflora* was not different between the fiddler crab addition and periwinkle removal treatment and the fiddler crab and periwinkle removal treatment, leading us to conclude that there are additional environmental stressors limiting the growth of *S. alterniflora*

at our study site. Stressors such as high salinities or low nutrient availability can prevent *S. alterniflora* from investing resources into new shoot production, particularly in the summer months (Smart and Barko 1980, Naidoo et al. 1992). As with other plants occurring in stressful environments, *S. alterniflora* may invest in live leaf tissue maintenance as opposed to new leaf production, except when actively losing live leaf tissue (e.g., via grazing) (Smith and Smith 2001, Lötscher 2006, Bortolus et al. 2004). When live leaf tissue is lost to grazing, the plant is forced to invest in more costly new leaf production rather than tissue maintenance (Smith and Smith 2001, Bortolus et al. 2004). In our study system, investment in new shoot production as a response to grazing losses appears to only be possible when fiddler crabs are present, as supported by positive change in stem height when fiddler crabs are present in conjunction with periwinkles, but negative change in stem height when only periwinkles are present (Fig. 2).

Previous studies have provided experimental evidence for two potential mechanisms by which fiddler crabs could facilitate *S. alterniflora* growth: sediment oxygenation via bioturbation, and nitrogen (N) biodeposition and redistribution within the sediment layers via deposit feeding and burrowing (Bertness 1985, Daleo et al. 2007, Holdredge et al. 2010). Bertness (1985) found that construction and maintenance of burrows by fiddler crabs oxygenated sediments and increased *S. alterniflora* production. This increase in production was coupled with a decrease in below-ground *S. alterniflora* debris (dead biomass) at a depth of 10-15 cm. At this depth, fiddler crab bioturbation has also been shown to increase oxygenation of sediments. Consistent with previous studies, we found that fiddler crab presence reduced total below-ground biomass, with the greatest difference being at a depth of 10-15 cm, and also maintained higher redox potentials at a depth of 10-15 cm in June, when compared to plots where fiddler crabs were removed (Fig. 1.3B-C). These results provide support for the hypothesis that bioturbation

allows plants to re-allocate resources to above-ground biomass production, and away from below-ground production. Bioturbation increases oxygen availability at depth, reducing the need for increased root and rhizome surface area for oxygen exchange (Howes et al. 1986). Increased oxygen availability could also allow for increased colonization of arbuscular mycorrhizal fungi, which can increase the availability of nitrogen to *S. alterniflora*, thus further reducing the need for below-ground biomass (Daleo et al. 2007).

An alternative explanation for the reduction in below-ground biomass in fiddler crab addition treatments could be that fiddler crab burrow construction may have disturbed and displaced *S. alterniflora* roots and rhizomes, thus reducing their total below-ground biomass. However, we did not observe an equivalent magnitude of reduction in below-ground biomass at shallower depths, where the greatest level of disturbance from burrowing is likely, because crabs spend much of their time close to the surface feeding and maintaining the entrance to their burrows (Fig. 1.3B, Christy 1982, Hemmi 2003). Because redox levels within all treatment (enclosed) plots were initially lower than the open (no enclosure) plots (Fig. 1.3C), it is possible that enclosure installation may have decreased redox potential. This decrease may have been caused by sediment compaction and severing of *S. alterniflora* clonal rhizomes along the plot edges associated with enclosure installation. However, all enclosed treatments experienced this initial drop in redox; therefore, differences would be due to treatment and not enclosure effects.

In addition to oxygenating the sediment through burrow construction and maintenance, fiddler crabs may also increase N availability to *S. alterniflora* through biodeposition and redistribution of N through the sediment layers. Salt marshes are often N-limited, therefore increases in N availability would likely enhance *S. alterniflora* production (van Wijnen and Bakker 1999, Silliman and Bortolus 2003). Holdredge et al. (2010) showed that biodeposition

and N redistribution by fiddler crabs may enhance S. alterniflora production in sandy, nutrientpoor salt marshes. Because net S. alterniflora growth was equivalent in fiddler crab addition plots and plots where both periwinkle and fiddler crabs were removed (Fig. 1.2), we hypothesized that there may be an additional constraint on S. alterniflora growth beyond lack of oxygen, such as N availability. To determine if the S. alterniflora growth could be N-limited at our study site, we measured new shoot N, C, and C:N (Table 1.B1). The observed lack of difference in N, C, and C:N in new S. alterniflora leaf tissue supports stress amelioration as the mechanism over increased nutrient availability via biodeposition. However, a reduction in below-ground biomass is also indicative of increased nutrient availability and leaf N concentration only provides an estimate of how much N is deposited into the leaves, rather than how much N is taken up by the plants (Smart and Barko 1980), therefore, we cannot rule out the possibility that both an increase in oxygen availability and nitrogen availability via fiddler crab bioturbation and biodeposition may have facilitated S. alterniflora growth. We acknowledge that the shorter duration of our experiment (two months as a result of Hurricane Irene) when compared to previous experiments testing the effects of different factors on S. alterniflora leaf N concentration (four-five months) may have affected our ability to detect differences in leaf N concentration between our treatments. However, increases in N availability (nitrate additions) have been shown to increase leaf N concentration by 2% or more within the first month of growth (Morris 1982), while the maximum difference in N concentration across our plots was less than 0.37% (Table 1.B1).

Field surveys revealed that although there was no difference in periwinkle densities between die-off fronts and continuous marsh, fiddler crab densities were lower along die-off fronts than in continuous marsh (Table 1.1). This could indicate that the effects of bioturbation

and biodeposition by fiddler crabs may be reduced along marsh die-off fronts and the higher density of dead *S. alterniflora* stems and shorter live stem heights along die-off fronts further supports this interpretation (Table 1.1). A reduction in *S. alterniflora* canopy cover (predation refuge) may reduce fiddler crab densities along die-off fronts (Hemmi 2003). Die-off fronts with high sediment anoxia, reduced standing live biomass, and high periwinkle densities may be susceptible to permanent marsh loss as a result of climate change (Kirwan and Murray 2007). *The role of facilitation in regulating top-down and bottom-up control of primary producers*

Our study provides empirical evidence that non-trophic facilitation can mitigate top-down control of S. alterniflora, thus potentially preventing the ultimate loss of the community dependent on this foundation species. Because top-down and bottom-up studies often focus solely on the organisms thought to be directly regulating standing biomass or production, the role of other co-existing species is often ignored. Understanding how both trophic (e.g., herbivory, predation) and non-trophic (e.g., stress amelioration, resource reallocation) interactions between organisms can alter community structure and function is critical to our understanding of ecosystem resilience to anthropogenic stressors such as habitat fragmentation, pollution, and global climate change (Bruno et al. 2003, Halpern et al. 2007, Kiers et al. 2010). Studies are needed to determine the prevalence and importance of facilitation effects on top-down and bottom-up regulation of primary producers, particularly for ecosystems where the primary producer also serves as a foundation species for numerous interconnected species (Stachowicz 2001), such as eastern hemlock (Tsuga canadensis) (Ellison et al. 2005), kelp (Egregia menziesii) (Hughes 2010), eelgrass (Zostera marina) (Hughes et al. 2009) and marsh cordgrass (S. alterniflora) (Bruno and Bertness 2001). Successful restoration and conservation of foundation species may be contingent upon facilitators, therefore monitoring of their abundance

and distribution should be incorporated into restoration and conservation efforts (Halpern et al. 2007). Salt marshes are highly productive ecosystems that are also susceptible to effects of climate change, particularly sea level rise and increased frequency of intense storm events (Mendelsohn et al. 2012, Morris et al. 2002). Non-trophic facilitation may increase salt marsh resilience to periwinkle grazing, which may be key to marsh survival in a changing climate.

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TABLES

Table 1.1. Surveys of *S. alterniflora* die-off fronts and the continuous short-form *S. alterniflora* regions of marshes within the Hoop Pole Creek Clean Water Reserve (HPC CWR) in Atlantic Beach, NC, and the Theodore Roosevelt Natural Area (TRNA) in Pine Knoll Shores, NC. Error bars present ± 1 SE (n=10).

	HPC CWR Marsh		TRNA Marsh	
Variable	Die-off	Continuous	Die-off	Continuous
Stem density (live stems/m ²)	252 ± 22	242 ± 18	184 ± 11	212 ± 13
Stem density (dead stems/m ²)	29 ^a ± 3	18 ^b ± 4	68 ^ª ± 8	21 ^b ± 6
Stem height (cm)	35.7 ^a ± 1.6	65.4 ^b ± 3.5	57.2 ^ª ± 2.7	70.2 ^b ± 3.3
Fiddler crab burrows (m ²)	59 ^ª ± 5	137 ^b ± 10	16 ^ª ± 6	98 ^b ± 31
Marsh periwinkles (m ²)	276 ± 28	220 ± 38	87 ± 8	85 ± 13
Sediment redox potential (mV)	-58.1 ± 24.3	-49.4 ± 32.9	-54.0 ± 9.9	-3.9 ± 32.7

^{a,b} Means with different letters (a or b) are significantly different within each site (P < 0.05, see Tables E1-2 for complete statistical analyses results).

FIGURES

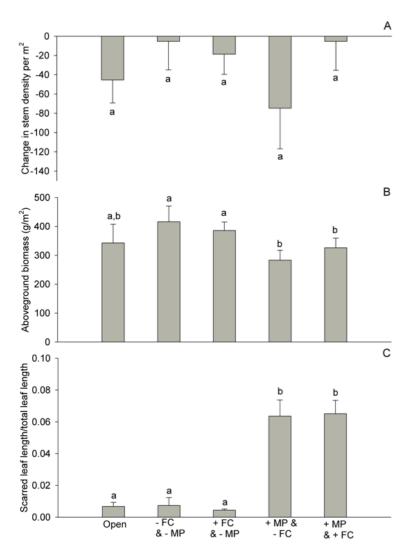


Figure 1.1. The effects of marsh periwinkle grazing on (a) *S. alterniflora* stem density, (b) *S. alterniflora* above-ground biomass, and (c) the proportion of scarred to live *S. alterniflora* leaf tissue. Treatments are as follows: open, fiddler crab and marsh periwinkle removal (– FC & – MP), fiddler crab addition and marsh periwinkle removal (+ FC & – MP), marsh periwinkle addition and fiddler crab removal (+ MP & – FC), and marsh periwinkle and fiddler crab addition (+ MP & + FC). Lowercase letters (a or b) above bars indicate treatments separated by planned comparisons (*see* Tables 1.C1-3). Error bars present ± or + 1SE (n=6).

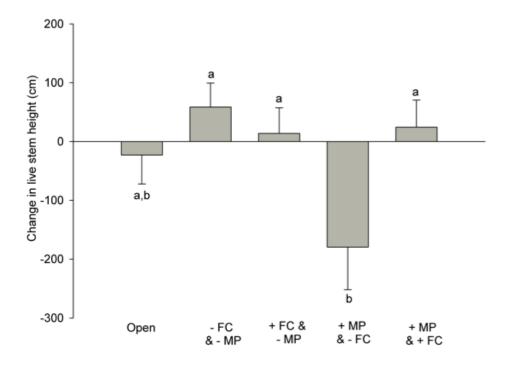


Figure 1.2. The effects of marsh periwinkle grazing and fiddler crab bioturbation on the change in *S. alterniflora* maximum live leaf height (net *S. alterniflora* growth) from the beginning to the end of the experiment. Treatments are abbreviated as in Figure 1. Lowercase letters (a or b) above bars indicate treatments separated by planned comparisons (*see* Table 1.C4). Error bars present \pm 1 SE (n=6).

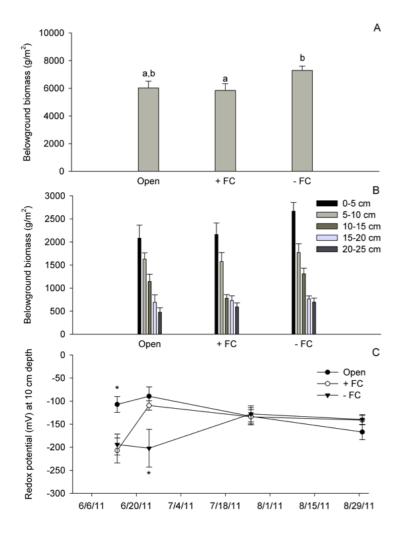


Figure 1.3. The effects of fiddler crab bioturbation on a) total *S. alterniflora* below-ground biomass (g/m²); b) *S. alterniflora* below-ground biomass (g/m²) at 0-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, and 20-25 cm depths; and c) the effects of fiddler crab bioturbation on sediment oxidation-reduction (redox, mV) potential at 10 cm depth. Fiddler crab addition (+ FC) and removal (– FC) treatments are pooled across periwinkle treatments. Lowercase letters (a or b) above bars in a) indicate treatments separated by planned comparisons (*see* Table 1.C5). An asterisk "*" in c) indicates treatments separated by planned comparisons (*see* Tables 1.D1-5). Error bars present \pm 1 SE (n=6 for open and n=12 for fiddler crab addition/removal treatments).

CHAPTER 2: ENGINEERING AWAY OUR FIRST LINE OF DEFENSE: AN ANALYSIS OF SHORELINE HARDENING IN THE UNITED STATES

Abstract

Rapidly expanding development associated with growing population centers along tidal riverine, estuarine and ocean coastlines is a primary driver of coastal habitat degradation and loss. Shoreline hardening in particular, often a byproduct of coastal development, results in the loss of coastal habitats and subsequent forfeiture of supported ecosystem services; yet it is a common practice along the coasts of industrialized countries. Here, we provide the first estimates of the percentage of hardened shoreline along open and sheltered coasts across the continental United States. Our analyses revealed that 22,842 km of U.S. shoreline (14% of total shoreline) has already been hardened, two-thirds of which is along the south-Atlantic and Gulf coasts. We also considered how environmental and socioeconomic factors such as housing density. storminess, and mean wave height, relate to the pervasiveness of shoreline hardening within U.S. coastal counties. Predictably, housing density was positively correlated with shoreline hardening throughout all three U.S. coasts. Along open coasts, high storm frequency (Atlantic) and low mean wave height (Pacific) were associated with increased hardened shoreline representation. The south Atlantic and Gulf sheltered coasts are likely the most vulnerable to future hardening based on projected coastal population growth rates and current coastal management policies. Simultaneously, these regions contain habitats that are highly vulnerable to erosion and loss associated with predicted relative sea-level rise and increased storminess. Federal and state

agencies should use these findings to inform coastal management policies and promote coastal ecosystem system resilience.

Introduction

Although coastal regions make up less than 4% of the Earth's total land area, coastal habitats, such as rocky shores, beaches, salt marshes, and mangroves (Figure 1A-D), are some of the most economically and ecologically valuable resources globally (Barbier et al. 2008, Millennium Ecosystem Assessment [MEA] 2005). Over one third of the human population lives within 100 km of a coastline and coastal population densities are continuing to increase in most regions of the world (MEA 2005, Woods Poole Economics, Inc. 2010). As coastal development increases with growing human population, adverse anthropogenic impacts are concentrating and intensifying within coastal ecosystems (Peterson et al. 2008a). Coastal development is vulnerable to damage and loss from coastal erosion, flooding, and destructive damage caused by rising sea levels, ambient wave energy, storms, and anthropogenic climate change (MEA 2005, Intergovernmental Panel on Climate Change [IPCC] 2014).

In the past century, mean sea level has risen between 0.1 and 0.25 m and is predicted to rise another 0.43 to 0.73 m by 2100 (IPCC 2014), while a 1.2 m rise in sea level is predicted for an unmitigated warming scenario (Horton et al. 2014). Elevated sea levels, augmented by increases in extremely high water levels from storm surge and localized winds during storms, astronomically driven high tides, and increased intensity and frequency of storms in some ocean basins (e.g., North Atlantic) are expected to dramatically modify shoreline sediment dynamics and the resultant geomorphology (IPCC 2014).

Historically, shoreline hardening has been a common societal response to coastal erosion, storm risks, and sea-level rise, particularly in industrialized countries with large coastal populations, such as the United States, the Netherlands, and Japan (Peterson et al. 2008b, Dugan et al. 2011, Walker and Mossa 1986). Shoreline hardening is defined as the construction or placement of vertical sea walls or bulkheads, sloped riprap (typically granite rocks, marl, or concrete rubble) revetments, groins, jetties, or breakwaters along or directly adjacent to a shoreline (Figure 2.1E-H). The extent and rate at which shorelines are being hardened has increased dramatically in the last century, in conjunction with growing coastal populations and increased development (Dugan et al. 2011). Although humans have been hardening the shoreline for hundreds of years in some regions of the world, the effects of shoreline hardening on coastal ecosystem function and supported services have only recently been considered by environmental and coastal managers (Chapman and Bulleri 2003, Dugan et al. 2011, National Research Council [NRC] 2007, Titus 1988).

Shoreline hardening on sandy beach coastlines can lead to displacement of dunes that naturally provide protection from storms, can steepen and reduce the width of the high beach available for burrowing invertebrates, and steepen and shorten the intertidal swash zone, which serves as habitat for benthic invertebrates, surf fishes, and shore birds (Dugan and Hubbard 2006, Dugan et al. 2008). Within sheltered coasts, sea walls and bulkheads lack the structural complexity of natural habitats such as marshes or rocks (Figure 2.1A,C,E,G), and thus support a reduced number of native benthic epibiota, fishes, and mobile invertebrates (Bilkovic and Roggero 2008, Bulleri and Chapman 2010, Gittman et al. *in review*, Seitz et al. 2006). When constructed landward of marshes and mangroves, shoreline hardening can also increase seaward

scour and prevent upslope transgression of these habitats during storm events and as sea level rises, thereby leading to their eventual loss (Dugan et al. 2011, Peterson et al. 2008a, Titus 1988).

Despite adverse effects of shoreline hardening on coastal ecosystem functions and ecosystem services, efforts to quantify how much of the world's coasts have been artificially hardened have been limited (Dugan et al. 2011). Current evaluations of the potential drivers of shoreline hardening have focused only on specific regions (e.g., Puget Sound, WA, Currin et al. 2009; Mobile Bay, AL, Scyphers et al. 2014) or hardening in response to a single event (e.g., 1900 hurricane in Galveston, TX, Hansen 2007). Some factors, including increasing coastal population densities and consequent development, have been proposed as drivers of shoreline hardening (MEA 2005, Peterson et al. 2008b). Coastal processes such as wave surge and local wind-driven waves during storms, tidal stage and lunar/solar positions, and sea level, as well as physical characteristics of the shoreline, such as slope, erosion rate, and geomorphology may also explain spatial patterns and temporal increases in shoreline hardening (NRC 2007, Ruggiero et al. 2001, USACE 2004). Finally, state-level coastal management policies related to shoreline hardening have been suggested to play a role in whether or not a shoreline is hardened (Titus et al. 1991, 1998, 2009). However, a national scale analysis of how these factors can collectively explain degree of shoreline hardening has not previously been conducted.

To date, no global estimate of the amount of shoreline that has been artificially hardened exists and estimates that encompass more than a single stretch of coastline (e.g., North Adriatic coast of Italy) are rare (Dugan et al. 2011). A national estimate of hardened shoreline is not currently available for the United States, despite its extensive coastline, high coastal population density (39% of the U.S. population lives in coastal counties), vulnerability to shoreline erosion, flooding, and property damage, and a growing national concern with the need for coastal

protection as climate changes (Arkema et al. 2013, MEA 2005, National Oceanographic and Atmospheric Administration [NOAA] 2013, Peterson et al. 2008b).

The purpose of this study is to: 1) estimate of the percentages of tidal, open and sheltered shorelines that have been artificially hardened in the continental U.S., 2) determine the relationship between shoreline hardening and physical and socioeconomic characteristics on a county-by-county scale using regression tree analyses; 3) identify regions of the U.S. likely to experience continued shoreline hardening and subsequent coastal habitat loss; and 4) identify future research directions and alternative management strategies for coastal protection.

Methods

Estimation of shoreline hardening along the U.S. coast

We used NOAA's Office of Response and Restoration (OR&R) Environmental Sensitivity Index (ESI) geodatabases to calculate the linear kilometers (km) of total shoreline and the linear km of hardened shoreline for each coastal county within the continental U.S. (see Appendix 2.A). NOAA ESI's were developed for evaluating the environmental impacts of oil spills on coastal habitats and species from multiple sources (e.g., aerial photographs, field surveys) and have been updated on a state-by-state basis since 2005 (Table 2.A1, NOAA 2005). The ESI dataset identifies 15 major shoreline types (e.g., Type 1: exposed rocky shore or sea wall) that are further subdivided into more specific shoreline types (e.g., Type 1A: exposed rocky shores 1B: exposed, solid man-made structures [sea walls], Figure 2.1A, E, Table 2.A2). We grouped all ESI shoreline types identified as man-made structures (sea walls, bulkheads, riprap structures [revetments, breakwaters, groins/jetties], and hybrid sea wall/bulkhead with riprap) to compute cumulative lengths of hardened shorelines (Figure 2.1 E-H, Table 2.A2). We then divided each state ESI shoreline dataset by coastal county and for the Pacific and Atlantic coast by whether the shoreline was "open" (i.e., directly exposed to the ocean) or "sheltered" (i.e., located in a bay, sound, or tidally influenced river). We did not divide the Gulf coast into open or sheltered coasts because much of the Gulf coastline consists of reticulated marsh and mangrove shoreline that cannot be clearly classified as open or sheltered (e.g., Louisiana coast and Big Bend region of Florida Gulf coast). Finally, we summarized the amount of hardened shoreline and tidal shoreline found in each coastal county (separately for sheltered and open Pacific and Atlantic coasts), and then calculated the percentage of hardened shoreline for each coastal county.

Regression tree analyses

To evaluate the relationship between environmental and socioeconomic factors and the percentage of hardened shoreline (sheltered or open or both) in each county along the Atlantic, Gulf, and Pacific coasts, we considered the following factors in regression tree analyses: housing density (units per km²), coastal slope (%), accretion/erosion rates (m/yr), geomorphology, mean tidal range (m), mean wave height (m), relative sea-level rise (mm/yr), storm frequency, relative county shoreline orientation (north to south or west to east along the coast), and years since a ban on shoreline hardening was passed. As a proxy for coastal population density, we used the 2010 density of individual housing units per km² for each coastal county, available from the U.S. Census Bureau. Physical shoreline characteristics (coastal slope, accretion/erosion rates, and geomorphology) as well as mean tidal range, mean wave height, and historical rates of relative sea-level rise, were acquired from the U.S. Geological Survey (USGS) Coastal Vulnerability Index (CVI) (see Supplemental Methods, Hammer-Klose and Thiehler 2001). To determine storm frequency, we summed the number of storms that resulted in a Presidential Major Disaster

Declaration or Emergency Declaration from 1970 to 2010 for each coastal county (Federal Emergency Management Agency [FEMA] 2014). We reviewed the current Federal and State legislation and permitting procedures related to coastal management and shoreline hardening to determine if and when states banned shoreline hardening on open and/or sheltered coasts (Table 2.A3). Although some states that prohibit shoreline hardening have exceptions that allow hardening of certain types of shoreline or conditions, (e.g., Virginia open coast ban), we assumed that this ban was in effect for a majority of the shoreline and thus input that information into the regression tree.

We ran separate regression trees for the Atlantic open and sheltered coasts, the Pacific open and sheltered coasts, and the Gulf coast, to describe differences among county level shoreline hardening patterns using repeated partitioning of those values into increasingly homogeneous groups across bimodal splits in the descriptor variables (De'ath and Fabricius 2000, McCune and Grace 2002). We developed regression trees using the analysis of variance (ANOVA) method of recursive partitioning and we pruned over-fitted trees using k-fold crossvalidation. Cross-validation estimated the relative predicted error for each tree size and the tree was pruned to the size (based on number of nodes) with the lowest cross-validation predicted error. We did not include the CVI variables in our regression tree analyses for the Pacific sheltered coast because of the majority of the sheltered shoreline on the Pacific coast did not have CVI data available (see Appendix A). All regression tree analyses were run using R version 3.1.0 (R Core Team 2014) and rpart (Therneau et al. 2014).

Results

Estimation of extent of shoreline hardening along the U.S. coast

The continental US was estimated to have 160,168 km of tidal shoreline, with 22,842 km (14%) of that shoreline hardened by bulkheads, sea walls, or riprap structures (Table 2.1, Figure 2.1E-H). On the open coasts of the Atlantic and Pacific, 846 km (9%) of the shoreline was hardened (Figures 2.2A and 2.3A). The states with the highest percentages of hardened shoreline (11 to 49%) on the Atlantic open coast were found north of Washington D.C. (Figure 2.2A, Table 2.A3). The counties of Suffolk, MA, Plymouth, MA, Rockingham, NH, Jasper, SC, and Monmouth, NJ, had the highest percentages of hardened shoreline on the Atlantic open coast (Table 2.2A). California had the most hardened shoreline on the Pacific open coast (Table 2.A3) with the following counties having the highest percentages (30% to 17%): Los Angeles, Orange, Ventura, San Diego, and Santa Cruz (Figure 2.3A).

Despite significant hardening of the shoreline on the open coast, shoreline hardening was more prevalent on sheltered coasts (Table 2.1). States with the highest percentages of hardening on the Atlantic sheltered coast include the District of Columbia (53%), Pennsylvania (36%), Connecticut (25%), Rhode Island (25%), and Florida (24%) (Table 2.A3). Some "hot spots" of hardening (> 80%) along the Atlantic sheltered coasts include the counties of New York, NY, Essex, NJ, Broward, FL, and Baltimore City, MD. The Atlantic coast had eight times as much sheltered shoreline, but only six times as much hardened shoreline as the Pacific coast, resulting in a higher percentage of hardened sheltered shoreline in the Pacific (18%) than in the Atlantic (13%) (Table 2.1, Figures 2.2B and 2.3B). California had the highest percentage of sheltered hardened shoreline on the Pacific coast (28%) and also had four of the five counties with the

most hardened shoreline (Los Angeles, San Francisco, Ventura, and Orange, 88% to 57% hardened).

The Gulf coast, excluding the extensive reticulated marshes of Louisiana, had the same percentage of hardened shoreline (insert %) as the open and sheltered Pacific coasts combined (this percentage drops to 9% when LA all potential marsh shoreline is included (Table 2.1, Figure 2.4, see Appendix 2.A). Texas had the highest percentage of hardened shoreline on the Gulf coast (20%), followed by Florida (17%) and Alabama (14%) (Table 2.A3). The counties of Orleans, LA, Harris, TX, Victoria, TX, Pinellas, FL, and Sarasota, FL, had the highest percentage of hardened shoreline (70% to 41%).

Regression tree analyses

On the Atlantic open coast, coastal counties that experienced 17 or more storm events that resulted in Presidential Major Disaster or Emergency Declaration from 1970 to 2010 (located in Massachusetts, Maine, and New Hampshire) had a higher percentage of hardened shoreline (μ = 30.7 ± 9.6%) than counties that experienced fewer than 17 storms (μ = 8.3 ± 1.4%, R² = 0.25, Figure 2.2A). In sheltered systems, Atlantic coastal counties with housing densities ≥ 658 units/km², or counties in southern Florida with housing densities ≥ 126 units/km², had the highest percentages of shoreline hardening (μ = 60.9 ± 4.8% and μ = 62.3 ± 14.5%, respectively, Figure 2.2B). When housing densities were < 126 units/km² or the county was not located in south Florida, fewer storms and a smaller mean tide range (m) were associated with a lower percentage of hardened shoreline per Atlantic coastal county. Housing density accounted for 41% of the variation in the percentage of hardened shoreline among counties along the Atlantic sheltered coast (R²=0.72, full regression tree).

The percentage of hardened shoreline along the Pacific open coast was higher (μ = 24.1 ± 2.8%) in counties where the mean wave height (m) was < 1.3 m (i.e., counties in southern CA) (Figure 2.3A). Counties with mean wave heights \geq 1.3 m and located south of San Francisco County, CA had more hardened shoreline (μ = 11.0 ± 2.7%) than counties north of San Mateo County, CA (μ = 2.4 ± 0.9%). Mean wave height accounted for 70% of the variance in percentage of hardened shoreline along the open Pacific coast ($R^2 = 0.80$, full regression tree). Consistent with the Atlantic sheltered coast, counties with high housing densities (\geq 316 units/km²) along the Pacific sheltered coast the also had the highest percentages of hardened sheltered shorelines (Los Angeles, San Francisco, and Orange Counties, CA, μ = 77.3 ± 10.1%, Figure 2.3B). When housing density was < 316 units/km² but ≥ 52 units/km², more frequent storms were associated with higher percentages of hardening ($\mu = 43.2 \pm 5.3\%$) than counties with the same housing densities but < 9 storms (Figure 2.3B). Counties with housing densities < 52 units/km² and experiencing fewer storms (< 5) also had a moderate percentage of hardened shoreline (Hood River, Wasco, and Sherman counties, OR, μ = 35.5 ± 2.3%) relative to counties defined by housing densities < 52 units/km² and > 5 storms. Housing density accounted for 60% of the variance in percentage of hardened shoreline along the sheltered Pacific coast ($R^2 = 0.81$, full regression tree).

On the Gulf coast, counties with greater housing densities (e.g., ≥ 91 units/km²) had higher percentages of hardened shoreline (e.g., μ = 41.7 ± 4.7%) than counties with lower housing densities (Figure 2.4). Counties with lower housing densities (< 14.5 units/km²) located in Texas had a higher percentage of hardened shoreline (μ = 9.2 ± 3.1%) than counties outside of Texas (μ = 3.7 ± 1.0%, Figure 2.4). Housing density alone partitioned 46% of the variation in the percentage of hardened shoreline on the Gulf coast (R² = 0.65, full regression tree).

Discussion

Shoreline hardening in the U.S.

Our analysis indicates that 14% of the U.S. shoreline is hardened and at least 64% (likely higher if the Gulf shoreline were included) of all hardened shorelines are located along sheltered coasts of estuaries, lagoons, and tidally influenced rivers (Table 2.1, Figure 2.2B and 2.3B). Shoreline hardening is a significant yet underappreciated action by which humans modify and degrade coastal ecosystems in the United States. Hardened shorelines, particularly sea walls and bulkheads, support reduced diversity and abundances of marine fauna when compared to natural shorelines, such as beaches and marshes, (Bilkovic and Roggero 2008, Dugan et al. 2008, Chapter 4: Gittman et al. *in review*, Seitz et al. 2006). Other coastal ecosystem services, such as nutrient processing and filtration (O'Meara et al. 2014), carbon storage (Pendelton et al. 2012) and recreational use (Kenchington 1993) can also be reduced by shoreline hardening. Given the prevalence and ecological consequences of shoreline hardening, steps should be taken to reduce the rate of shoreline hardening and to identify areas where shoreline hardening should be avoided.

Potential drivers of shoreline hardening in the United States

Understanding the potential drivers of shoreline hardening could help understand where and how much shoreline and associated habitats are at risk of being hardened in the near future. Our analyses revealed that housing density was the single most importance factor associated with shoreline hardening on U.S. Atlantic and Pacific sheltered coasts, as well as the entire Gulf coast. Globally, shoreline hardening is associated with densely populated coastlines (e.g., Mediterranean coastline), and has been used to protect coastal development and infrastructure for centuries (Charlier et al. 2005). Most major coastal U.S. metropolitan areas are located on

sheltered coasts and tend to be heavily hardened (e.g., New York, Miami, Los Angeles, New Orleans) regardless of any other physical shoreline characteristics or processes. However, housing density alone may not represent all coastal development associated with major metropolitan areas.

To account for "neighbor" effects among counties that could be related to development "sprawl" from major population centers, we also included the north to south and west to east order of each coastal county. South Florida, Texas, and the northeast have major coastal metropolitan areas (e.g., Miami, Houston, New York, Boston) that support other types of development in neighboring coastal counties (e.g., fishing industry, seasonal housing) that may contribute to shoreline hardening despite relatively low housing density in those neighboring counties (Figure 2.2B, 2.3B, and 2.4, NOAA 2013). These areas also have a history of coastal modification that extends beyond city centers to include dredging of waterways and canals to support shipping traffic from major ports (New York, Corpus Cristi, Miami) and for flood control (construction of south Florida canal systems) that may also contribute to higher amounts of hardening in these regions (U.S. Census Bureau 2010, South Florida Water Management District 2014). On the Pacific open coast, neighbor effects may also be important, with higher percentages of hardening occurring in southern California counties than counties north of San Mateo County (Figure 2.3A). Southern CA has numerous ports and support infrastructure for major metropolitan areas (San Francisco, Los Angeles) that could contribute to shoreline hardening in this region more so than local housing density.

Outside of extensively hardened metropolitan areas, shoreline hardening became more closely related to the vulnerability of coastal development to loss and damage. On the Pacific open coast, wave heights were the most important factor related to shoreline hardening, with

smaller wave heights associated with more hardening than areas with large wave heights (Figure 2.3A). Wave heights above 1.3 m are associated with rocky shorelines and bluffs of northern California, Oregon and Washington and may not be suitable for most coastal development (Figure 2.3A). However, wave height is also strongly positively correlated with county location $(R^2 = 0.82)$ and years post-shoreline hardening ban $(R^2 = 0.67)$. California counties had an order of magnitude more shoreline hardening (12%) on the open coast than Oregon or Washington (1% each), which both have bans on shoreline hardening (Table 2.A3). Because the regression tree selects a single variable that reduces the most variance in shoreline hardening (%), county location and years post-ban may have been methodologically excluded from the tree despite being related to hardening.

Storm frequency was the most important predictor of shoreline hardening on the Atlantic open coast and also predicted shoreline hardening on both the Atlantic and Pacific sheltered coasts (Figures 2.2 and 2.3). Greater storm frequency generally resulted in a higher percentage of hardening on each coast. Shoreline hardening often occurs in reaction to damage and erosion from major storm events (e.g., seawall construction in Galveston, TX, following a major hurricane in the early 20th century, Hansen 2007); therefore areas prone to major storms would be expected to have more hardened shoreline. However, the relative efficacy of shoreline hardening in protecting the shoreline from erosion during storm events when compared to natural beach dune and marsh shoreline has been questioned. For example, sea walls and riprap structures were overwashed, while dunes remained in tact during a Category 4 hurricane on the open coast of South Carolina (Thieler and Young 1991) and bulkheads failed and suffered significant damage, while marsh shoreline should no evidence of shoreline erosion during a Category 1 hurricane on the sheltered coast of North Carolina (Chapter 3: Gittman et al. 2014).

Given the poor performance of shoreline hardening structures during these storm events, the use of shoreline hardening structures in response to storms should be evaluated further.

Predictions for future hardening and associated habitat loss

Although many European countries have been hardening their shorelines for centuries, a majority of the hardening of the U.S. shoreline likely occurred within the last 100 years (Charlier et al. 2005). Assuming that most shoreline hardening occurred after 1900 (when the U.S. Army Corps of Engineers [USACE] began to address coastal erosion at large scales), the historic rate of shoreline hardening in the U.S. would be > 200 km per year. If this rate of hardening were to remain constant and coastal populations were to continue to increase, the percentage of hardened shoreline would likely double by the year 2100, resulting in nearly one third of U.S. coastlines being hardened. This projected rate assumes that no additional restrictions are placed on shoreline hardening. Currently only eight coastal states have implemented total or partial bans on shoreline hardening and the efficacy of these bans has varied from state to state (Tables 2.A3). Otherwise, this projected rate of hardening of 200 km per year is likely conservative given the projected acceleration in population growth along the coast (NOAA 2013, Table 2.A3).

Some of the largest increases in population density are predicted for south Atlantic and Gulf coasts states, which is also where most of the U.S.'s remaining tidal salt marsh (> 50%) and mangrove areas (100%) occur (Dahl 2011, Kennish 2001). As much as 50% of U.S. salt marsh has been lost in the last century, largely as a result of human activities (Kennish 2001). The most recent losses of salt marsh (2.8%) between 2004 and 2009 were attributed to effects from coastal storms, land subsidence, global sea level rise, or other ocean processes, with a majority of these losses occurring in Louisiana and Texas (Dahl 2011). Increases in shoreline hardening combined with projected increases in storm frequency and intensity (IPCC 2014) along shorelines

containing marsh or mangrove are likely to increase the rate of loss of these habitats. Our finding that many coastal counties along the mid- to south-Atlantic coast are vulnerable to future coastal habitat loss is similar to the findings of Titus and colleagues: 60% of the land below 1m sea level on the Atlantic coast is expected to be developed and hardened, thus inducing widespread and substantial coastal habitat loss with future sea level rise, commonly referred to as "coastal squeeze" (Titus et al. 2009, Doody 2004).

Current shoreline hardening policies and permitting

Although we did not find any obvious relationship between state-level prohibition of shoreline hardening and the percentage of hardened shoreline in affected counties, shorelinehardening policies may still be important drivers of future hardening. While some of the open coast bans on shoreline hardening were proactive and occurred before much hardening took place (e.g., North Carolina, South Carolina, Oregon), other bans were likely reactionary (e.g., Rhode Island) and occurred after much of the shoreline had been hardened (Table 2.A3). Additionally, some bans have exceptions that have allowed for continued hardening of the shoreline in some regions (e.g., Virginia and Oregon open coasts). Finally, a ban on shoreline hardening is the most extreme restriction on shoreline hardening, with many states having lesser restrictions (e.g., Maryland allows shoreline hardening, but requiring "living shorelines" [stabilization that includes a living component such as marsh planting] to be used in lieu of pure hardening, whenever feasible [Maryland Department of Natural Resources 2006]). Enforcement and interpretation of many state shoreline-hardening regulations is inconsistent and often ineffective (Good 1994), which undoubtedly leaves much of the U.S. shoreline vulnerable to future hardening.

Recommendations for future research and coastal management strategies

This assessment reveals that much of the U.S. coastal shoreline is vulnerable to future habitat loss if actions are not taken to address scientific, regulatory, and educational gaps in current coastal management strategies. Additional research is needed on the long-term effects of shoreline hardening on coastal habitats, particularly on the ability of those habitats to transgress as sea level rises, and on the performance of traditional shoreline hardening relative to alternative options (e.g., living shorelines) in response to storm events, sea-level rise, and ambient wave energy (see Gittman et al. 2014). Continued updating of current shoreline hardening estimates is needed to determine present-day rates of hardening. Coastal management agencies and planners could then use these rates to assess the cumulative impacts of shoreline hardening on coastal habitats and to assess the risk of future habitat loss. Federal and state policy makers should use these assessments to develop informed, sustainable shoreline hardening legislation and permitting regulations, which should include revising the USACE nationwide permits to account for the future loss of habitat beyond the construction footprint for shoreline hardening placed landward of vulnerable coastal habitats (see Titus et al. 2009, Peterson et al. 2008b). Finally, we recommend a coordinated effort between Federal and state agencies to develop new guidelines for coastal management that incorporate green infrastructure and planning for shoreline migration and habitat egress (e.g., rolling easements, bulkhead removal) as sea level rises.

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TABLES

Region	Total Shoreline (km)	Hardened Shoreline (km)	Hardened (%)
Atlantic	99,494	12,923	13
Sheltered	93,848	12,425	13
Open	5,646	498	9
Gulf ^{a,b}	44,939	7,390	16
Pacific	15,735	2,529	16
Sheltered	12,026	2,182	18
Open	3,709	348	9
Total	160,168	22,842	14

Table 2.1. Summary of shoreline hardening estimates for continental U.S. coasts

^aThe Gulf shoreline could not be divided into "Open" and "Sheltered" coasts due to the reticulated nature of the shoreline along several of the LA and FL coastal counties.

^bThe shoreline estimates for the Gulf do not include a majority of the reticulated marsh shoreline in Louisiana because this shoreline was not included in the LA ESI geodatabase, resulting in an underestimate of the total and hardened shoreline for the Gulf. If the NOAA shoreline for LA (circa 1986) is used as an estimate of total shoreline in LA and we assume the approximately 1,000 of hardened shoreline has not been classified (based on aerial imagery), then the total Gulf shoreline would be 90,886 km and the total hardened shoreline would be 8,390 km. This would change the percentage of hardened shoreline for the Gulf to 9% and for the U.S. to 12%. See Supplemental Methods for additional information on estimating the shoreline in LA.

FIGURES



Figure 2.1. Types of natural and artificially hardened shorelines found in the Untied States: a) rocky shore; b) beach; c) tidal marsh; d) mangrove; e) sea wall; f) riprap revetment; g) bulkhead; and h) breakwater. For images of other shoreline types found in the U.S., refer to the NOAA ESI shoreline types image gallery (http://response.restoration.noaa.gov/esi-shoreline-types).

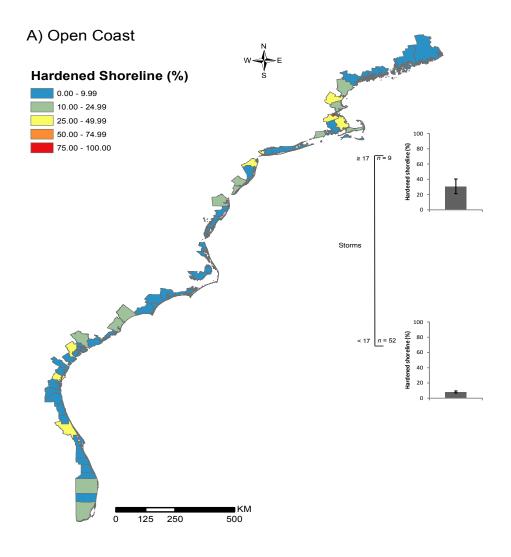


Figure 2.2A. The percentage of total tidal shoreline hardened by county and the regression tree results for the Atlantic open coast. "Housing Density" is the number of individual housing units per km² (as defined by the U.S. Census Bureau), "Storms" are the total number of storms that resulted in a U.S. Presidential Major Disaster Declaration and/or Emergency Declaration from 1970-2010, "Tide" is the mean tide range (m), "State" is the state in which the shoreline is found, and "n" is the number of counties split into each node and used to calculate the percentage of hardened shoreline.

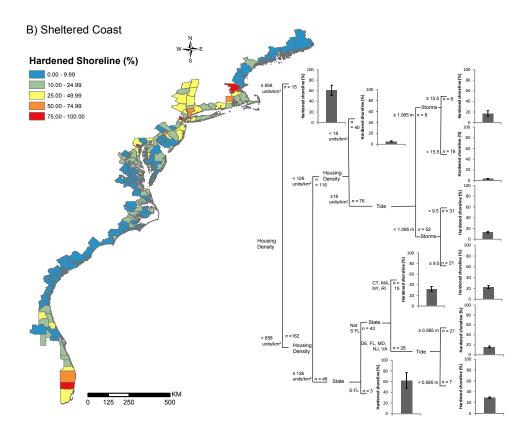


Figure 2.2B. The percentage of total tidal shoreline hardened by county and the regression tree results for the Atlantic sheltered coast. "Housing Density" is the number of individual housing units per km² (as defined by the U.S. Census Bureau), "Storms" are the total number of storms that resulted in a U.S. Presidential Major Disaster Declaration and/or Emergency Declaration from 1970-2010, "Tide" is the mean tide range (m), "State" is the state in which the shoreline is found, and "n" is the number of counties split into each node and used to calculate the percentage of hardened shoreline.

A) Open Coast

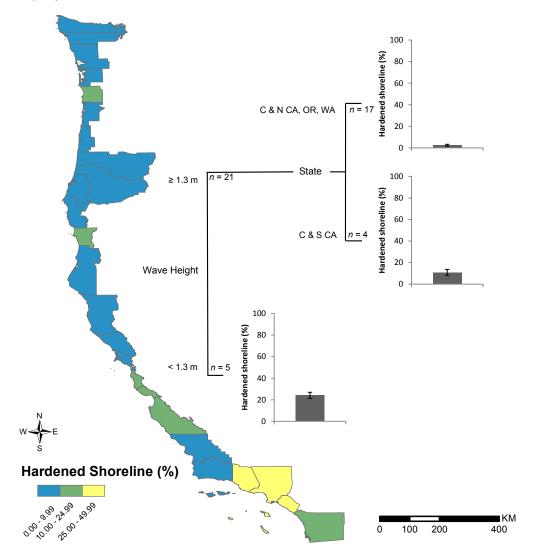


Figure 2.3A. The percentage of total tidal shoreline hardened by county and the regression tree results for the Pacific open coast. "Wave Height" is the mean wave height (m). "State", "Housing Density", "Storms", and "n" are defined as in Figure 2.2.

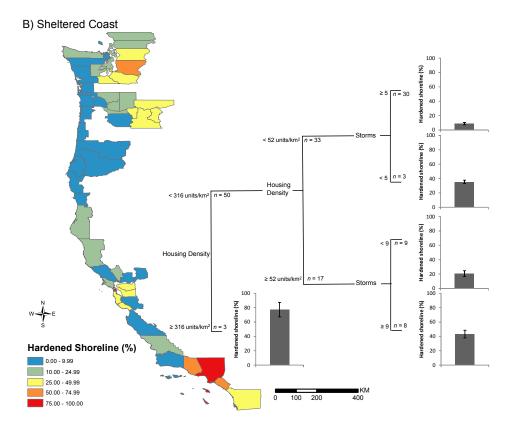


Figure 2.3B. The percentage of total tidal shoreline hardened by county and the regression tree results for the Pacific sheltered coast. "Wave Height" is the mean wave height (m). "State", "Housing Density", "Storms", and "n" are defined as in Figure 2.2.

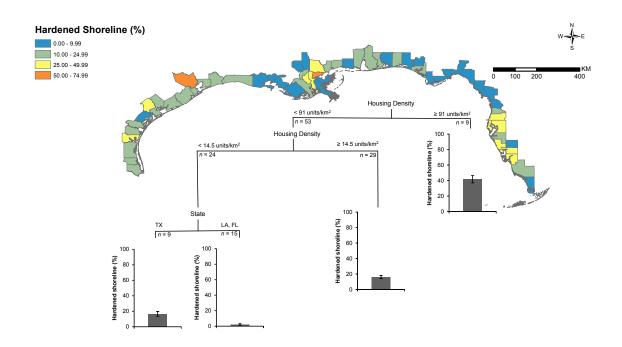


Figure 2.4. The percentage of total tidal shoreline hardened by county and the regression tree results for the Gulf coast. "Housing Density, "State", and "n" are defined as in Figure 2.2.

CHAPTER 3: MARSHES WITH AND WITHOUT SILLS PROTECT ESTUARINE SHORELINES FROM EROSION BETTER THAN BULKHEADS DURING A CATEGORY 1 HURRICANE²

Abstract

Acting on the perception that they perform better for longer, most property owners in the United States choose hard engineered structures, such as bulkheads or riprap revetments, to protect estuarine shorelines from erosion. Less intrusive alternatives, specifically marsh plantings with and without sills, have the potential to better sustain marsh habitat and support its ecosystem services, yet their shoreline protection capabilities during storms have not been evaluated. In this study, the performances of alternative shoreline protection approaches during Hurricane Irene (Category 1 storm) were compared by 1) classifying resultant damage to shorelines with different types of shoreline protection in three NC coastal regions after Irene; and 2) quantifying shoreline erosion at marshes with and without sills in one NC region by using repeated measurements of marsh surface elevation and marsh vegetation stem density before and after Irene. In the central Outer Banks, NC, where the strongest sustained winds blew across the longest fetch; Irene damaged 76% of bulkheads surveyed, while no damage to other shoreline protection options was detected. Across marsh sites within 25 km of its landfall, Hurricane Irene had no effect on marsh surface elevations behind sills or along marsh shorelines without sills.

²This chapter was previously published as an article in *Ocean & Coastal Management*. The original citation is as follows: Gittman R.K., Popowich A.M., Bruno J.F., and Peterson C.H. 2014. Evaluation of shoreline protection approaches during a hurricane: poor performance of bulkheads implies need for alternative protection strategies. Ocean and Coastal Management 102: 94-102. DOI: 10.1016/j.ocecoaman.2014.09.016

Although Irene temporarily reduced marsh vegetation density at sites with and without sills, vegetation recovered to pre-hurricane levels within a year. Storm responses suggest that marshes with and without sills are more durable and may protect shorelines from erosion better than the bulkheads in a Category 1 storm. This study is the first to provide data on the shoreline protection capabilities of marshes with and without sills relative to bulkheads during a substantial storm event, and to articulate a research framework to assist in the development of comprehensive policies for climate change adaptation and sustainable management of estuarine shorelines and resources in U.S. and globally.

Introduction

Global climate change, resulting largely from anthropogenic greenhouse gas emissions, is causing the oceans to expand as waters warm and receive additional freshwater from melting glaciers and ice caps, producing rising sea levels. The global rate of sea-level rise is accelerating (Church et al. 2008), and will likely continue to accelerate as the climate continues to warm (Nicholls and Cazenave 2010). Sea-level rise will require shoreline ecosystems, such as coastal marshes, either to accrete vertically or to transgress landward to higher elevations to persist. Additionally, climate change may result in an increase in the frequency of intense storm events, particularly hurricanes (Grinsted et al. 2013), and cause significant damage to coastal structures and erosion of shorelines (Thieler and Young 1991). Coastal marshes act as natural buffers to wave energy and inhibit erosion of coastal lands (Barbier et al. 2008, Meyer and Townsend 1997, Shepard et al. 2011). Nevertheless, these marshes are at great risk from degradation and loss as sea-level rise and increased storminess interact with coastal development and associated

shoreline hardening (Grinsted et al. 2013, Nicholls and Cazenave 2010, Peterson et al. 2008a,b, Rahmstorf 2010, Titus et al. 2009).

Shoreline hardening, the installation of man-made shoreline protection structures, is intended to protect coastal property from erosion caused by ambient winds, boat wakes, and storm events (Titus 1998). On the U.S. Atlantic coast, vertical asbestos, treated wood, composite plastic, or steel bulkheads (Fig. 3.1A), sloping stone, marl, or concrete riprap revetments (Fig. 3.1B), or a combination of riprap revetment and bulkhead (referred to as hybrid herein) are constructed at or above the observed high-water mark (OHWM), which is typically landward of regularly inundated, coastal marshes (United States Army Corps of Engineers [USACE] 2004). Because of their fixed position relative to coastal marshes, bulkheads and riprap revetments have the potential to inhibit upslope transgression of marshes as sea level rises (Peterson et al. 2008b, Titus 1988). This may ultimately lead to the loss of coastal marsh habitats and their ecosystem services, including nutrient and pollutant filtration, habitat provision for fishes and crustaceans, and erosion prevention (Peterson et al. 2008a). For coastal policies to be comprehensive in providing storm protection for estuarine land owners, while also preventing or minimizing degradation and loss of coastal habitats, the following scientific and engineering information on each shoreline protection approach is needed and is currently lacking or incomplete: (1) relative shoreline protection capabilities; (2) cost effectiveness; (3) ecological effects; and (4) reversibility and adaptability if the approach results in the eventual violation of applicable laws (e.g., Clean Water Act [CWA]) as sea-level rise threatens to drown tidal marshes (Titus 1998).

Bulkheads and riprap revetments are the dominant method of shoreline protection in North Carolina and many other coastal states (National Research Council [NRC] 2007). Many property owners assume that bulkheads provide superior shoreline protection from erosion and

storm damage compared to other methods (Fear and Currin 2012, Scyphers et al. 2014). However, studies comparing the shoreline protection provided by marshes and marshes with sills to traditional shoreline protection methods are lacking, particularly during storms (see Shepard et al. 2011). A sill is a shoreline protection structure typically constructed of low-rising granite, marl, or oyster shell placed well below OHWM and 1-2 m seaward of regularly inundated marsh macrophytes (Fig. 3.1C). Incomplete knowledge of the ecosystem effects and adaptability of each alternative shoreline protection approach has resulted in conflicting permitting policies for shoreline protection among the individual districts of the United States Army Corps of Engineers (USACE) and between states. For example, in North Carolina, bulkheads can be exempt from USACE review, via use of Nationwide Permit (NWP) 13, and are often permitted in fewer than two days by the North Carolina Division of Coastal Management (NC DCM). Sills, because of their position relative to OHWM, are not exempt from USACE review. Hence, permitting in North Carolina can take 30 to 120 days or longer (NC DCM 2012). However, the Baltimore, Maryland, USACE District does not recognize NWP 13 and the Maryland Department of Natural Resources (MD DENR) requires that marsh planting with or without sills be used in lieu of bulkheads (Titus et al. 2009). To produce estuarine shoreline protection policies within states and nations that maximize benefits and minimizes losses, new studies are needed that address the relative shoreline protection capabilities, costs, ecological effects, and reversibility and adaptability of various shoreline protection approaches.

The hypothesis that bulkheads, riprap revetments, marshes with sills, and marshes without sills, differ in their ability to protect the shoreline from erosion during a storm event was tested during Hurricane Irene. Coastal North Carolina is a relevant location in which to test this hypothesis because the NC coast has been affected by nearly 100 tropical storms or hurricanes

since 1851 and as much as 5900 km² of the coastal land in North Carolina is expected to be inundated by 2100 under a projected sea level rise of 1.1 m (NC State Climate Office 2014, Poulter et al. 2009). Our study included: 1) visual classification of the extent of shoreline damage as a function of shoreline protection type over long extents of the back-barrier shorelines of Bogue Banks and the Outer Banks, NC, immediately after passage of Hurricane Irene; and 2) erosion analysis of marshes with and without sills along Bogue Sound, NC, before and after Hurricane Irene. The resulting shoreline-protection evaluation data represent the first empirical progress within a larger framework of information necessary for developing comprehensive and sustainable coastal management policies for estuarine shorelines.

Methods

Description of study sites

Visually apparent damage to bulkheads, riprap revetments, and marshes with sills was recorded within one month of landfall of Hurricane Irene in North Carolina (Fig. 3.2A). Landfall occurred at Cape Lookout, NC, on August 27, 2011 as a Category 1 Hurricane, with a sustained wind-speed of 38 m/s. The strongest winds were primarily to the east of the eye over Pamlico Sound and the Outer Banks (Avila and Cangialosi 2011). Approximately 14 km of back-barrier shoreline on the Outer Banks were surveyed within the towns of Rodanthe, Waves, and Salvo on the north end of Hatteras Island (Fig. 3.2B), as well as approximately 38 km of shoreline within Frisco and Hatteras Village on the southern end of Hatteras Island, NC (Fig. 3.2C-D). Hatteras Island is a barrier island approximately 320 km in length, bordered by Pamlico Sound to the west and the Atlantic Ocean to the east. Approximately 25 km of back-barrier estuarine shoreline on Bogue Banks (Fig. 3.2E) were also surveyed. Bogue Banks is a south-facing barrier island

approximately 34 km in length, bordered by Bogue Sound to the north and the Atlantic Ocean to the south and the surveyed shoreline on Bogue Banks is situated within 25 km of the Irene landfall.

To determine if marsh with sills or marshes without sills would protect coastal property from erosion during a storm event, three marshes with sills and three unmodified marshes were evaluated in Pine Knoll Shores, NC, bordering Bogue Sound (Fig. 3.2E). At each sill site, a sill consisting of piled granite boulders (diameter of 20 cm to 50 cm) had been constructed between the years of 2002 and 2007. The elevation of the top of each sill was between 0.14 and 0.31 m above mean sea level (MSL). Each sill had an average height ranging from 0.2 m (base to top of the sill) for the oldest to 0.56 m for the youngest sill. Marsh grasses, *Spartina alterniflora* and *S. patens*, had been planted behind each sill along the edge of existing marsh at elevations consistent with the positions of these two grasses on nearby unmodified marshes. A reference marsh site was selected near each sill site (Fig. 3.2E), based on physical similarity (similar marsh size, shoreline orientation, and elevation) and proximity (within 500 m) to the sill site (sensu Neckles et al. 2002).

Damage assessment of shoreline protection structures

Using a Trimble GeoExplorer (2008 series), GPS points were recorded at the beginning and end of each continuous stretch of each shoreline protection type. We recorded the presence or absence and category of damage for each shoreline stretch. Damage classifications were modified from Thieler and Young (1991) and were as follows: landward erosion; structural damage; breach; and collapse. Landward erosion was defined as erosion of the shoreline landward of the structure (Fig. 3.3A). Structural damage was defined as warping or evident damage to the structure without breach or collapse (Fig. 3.3B). A breach was defined as a gap or

hole visible in the structure that allowed landward sediment to escape (Fig. 3.3C), while a collapse was defined as complete loss of the integrity of the structure so that it was no longer effectively retaining any sediment landward (Fig. 3.3D). Photographs were taken of each shoreline protection type (e.g., bulkhead, riprap revetment, sill) and each instance of damage to a shoreline protection structure. GPS data were imported into ArcGIS as shapefiles. Shapefiles were overlaid on 2010 aerial orthoimagery (North Carolina One Map 2013) and digitized shorelines of Bogue Banks and the Outer Banks (NC DCM 2012). NC DCM classified NC shorelines using 2007 aerial orthoimagery for Dare and Hyde counties and 2010 aerial orthoimagery for Carteret County (where Bogue Banks is located), producing ArcGIS continuous line shapefiles that include the shoreline type (marsh, beach, modified with structure [hardened]) and shoreline structure type (boat ramp, bulkhead, bulkhead and riprap combined, breakwater, groin/jetty, sill, riprap revetment).

A new line shapefile was created based on the NC DCM digitized shorelines and the NC DCM shoreline classifications were verified using GPS points, shoreline photos, and field notes. The NC DCM digitized shoreline associated with each set of GPS points (start and end of each stretch) was classified according to shoreline protection type and damage category recorded during the survey. If our surveyed shoreline classification did not agree with the NC DCM classified the shoreline as a bulkhead and NC DCM classified the shoreline as a bulkhead and NC DCM classified the shoreline as a marsh), the known shoreline classification based on survey data was chosen and the NC DCM shoreline classification was corrected. The total linear km of shoreline surveyed by shoreline protection type and the total linear km of shoreline damaged by category and by shoreline protection type for each region were then calculated.

Erosion analysis of marshes with and without sills

Changes in marsh surface elevation and marsh macrophytic vegetation density during and after Hurricane Irene were determined for marshes with sills and without sills. Pre-Irene surveys were conducted in August 2010 (one year before) and post-Irene surveys in October 2011 (one month after) and October 2012 (13 months after). Surface elevation (\pm 5 mm) was measured along permanent transects at each site using a leveling rod and rotary laser level and referencing the measurements to semi-permanent benchmarks (points established on a stable structure with unchanging elevation, e.g., a piling or tree). Elevations relative to North American Vertical Datum of 1988 (NAVD88) were determined using a Trimble Virtual Reference Station (VRS), Real Time Kinematic (RTK), Global Positioning System (GPS). NAVD88 elevations obtained using these methods are estimated to be accurate to \pm 6-10 cm (C. Currin 2013 *personal communication*). Five transect locations were selected using restricted random (between 10 m and 20 m apart to maintain independence) sampling (sensu Neckles et al. 2002). Marsh transects began at the water's edge of the marsh and continued to the start of shrub-scrub vegetation or to property owner landscaping. Marsh plots (0.25 m^2) were established at 3 or 5 m intervals along each transect beginning at the lower marsh edge and surface elevation was measured within each plot. The length of each transect (5 - 20 m) and total number of marsh plots established (9 - 21)depended on the marsh width from water's edge to upland vegetation at each site. To compare marsh vegetation density between marshes with and without sills and to determine the changes in density over time, plant stem density was measured by species per 0.25-m² plot.

Mixed effects models were fit using restricted maximum likelihoods to determine if marsh surface elevation and stem density in marshes with and without sills changed in the short term (<1 month) or long term (13 months) as a result of Hurricane Irene. Treatment (marsh with

sill vs. marsh without sill), year (2010, 2011, and 2012), and distance from the lower marsh edge, were fixed effects, while site was a random effect. Tukey's posthoc tests were used to evaluate differences in levels of significant factors. Data were Box-Cox transformed prior to analysis to meet the assumptions of homogeneity of variance (Levene's test, P > 0.05). An alpha level of 0.05 was used for all hypothesis testing. Analyses were conducted using JMP 10.0 (SAS 2012).

Results

Damage assessment of shoreline protection structures

Of the 76 km of shoreline surveyed along the back-barriers of Hatteras Island and Bogue Banks, 28 km (37%) of the shoreline was protected by bulkheads. Riprap revetments, sills, and hybrid methods were less common than bulkheads, making up only 1.9%, 1.6%, and 2% of the shoreline, respectively, while the remaining shoreline was marsh (53%) or beach (3%) (*see* Fig. 3.4A for km of shoreline protection types by survey region).

Of the 1.86 km of bulkheads surveyed in Rodanthe, Waves, and Salvo (Fig. 3.4A), 76% (1.41 km) was damaged after the Hurricane (Fig. 3.4B), with damage ranging from landward soil erosion (Fig. 3.3A) to complete bulkhead collapse (Fig. 3.3D). In contrast, only 4% (0.26 km) of the 7 km of bulkheads surveyed in Frisco, 9% (0.83 km) of the 9 km of bulkheads in Hatteras Village, and 12% (1.14 km) of the 9.77 km of bulkheads on Bogue Banks (Fig. 3.4A) was damaged (Fig. 3.4B). No visible damage (structural failure, landward soil erosion) was detected to sill, riprap revetment, or hybrid shoreline structures surveyed within the study regions. *Erosion analysis of marshes with and without sills*

Mean marsh surface elevations were significantly higher at sites with sills than at marsh sites without sills across all years (P = 0.001, Table 3.1, Fig. 3.5A). Elevation increased with

increasing distance from the lower marsh edge, with the change in elevation being greater from the edge to the upland marsh at sites without sills than at sites with sills (P < 0.001). However, a significant change in marsh surface elevation was not detected from August 2010 (before Hurricane Irene) to October 2011 (one month after Hurricane Irene) at marshes with or without sills nor was a significant change detected in marsh surface elevation from October 2011 (immediately after Hurricane Irene) to October 2012 (13 months after Hurricane Irene) (P =0.930, Fig. 3.5A). There were no significant interactions between treatment and year or treatment, year, and distance from marsh edge (P > 0.05).

Vegetation density did not vary between marshes with sills and marshes without sills (P = 0.078, Table 3.1, Fig. 3.5A), but did increase with increasing distance from the marsh edge (P = 0.007). From August 2010 (before Hurricane Irene) to October 2011 (after Hurricane Irene), vegetation density decreased by 167 ± 86 stems m⁻² within marshes with sills and by 154 ± 73 stems m⁻² within marshes without sills respectively, (P < 0.05, Tukey's post hoc tests, Fig. 3.5B). Increases of 218 \pm 98 macrophyte stems m⁻² within marshes with sills and 42 \pm 59 macrophyte stems within marshes without sills, respectively, occurred from October 2011 (immediately after Hurricane Irene) to October 2012 (13 months after Hurricane Irene) (P < 0.05, Tukey's post hoc tests, Fig. 3.5B). In 2010 and 2012, vegetation density was not significantly different across sites (P > 0.05, Tukey's post hoc tests, Fig. 3.5B). However, while vegetation within marshes with sills in 2012 appeared to have recovered to 2010 levels, within marshes without sills, the marsh did not appear to recover to the same vegetation density over this time period, although this difference in recovery was not statistically significant (P = 0.289, Fig. 3.5B). There were no significant interactions between treatment and year or treatment, year, and distance from marsh edge (P > 0.05).

Discussion

The purpose of a shoreline protection structure is to prevent erosion of shoreline and damage to coastal property during storm events, such as hurricanes (USACE 2004). Engineering performance and cost efficiency and are among key deciding factors for coastal property owners when choosing a shoreline protection approach (Scyphers et al. 2014), whereas ecological effects relative to current environmental regulations are important factors for coastal managers charged with permitting shoreline protection structures (Titus 1998). Hence, data on the shoreline protection capabilities, cost efficiency, effects on ecosystem services, and reversibility and adaptability of alternative shoreline protection approaches are critical to development of economically and ecologically sound coastal management policies.

Shoreline protection capabilities

Results of our post-Hurricane Irene damage surveys conducted along shorelines at Rodanthe, Waves, and Salvo, NC, indicated that at least 75% of sampled bulkheads were damaged (Fig. 3.4B). The percentage of bulkheads damaged within other surveyed regions was far lower, ranging from 4 to 10%. Rodanthe, Waves, and Salvo experienced a greater storm surge (2.16 m) and longer period (30 hours) of sustained onshore winds greater than 17 m/s (minimum speed for tropical depression) than our other survey regions (Table 3.2) (National Oceanographic and Atmospheric Administration [NOAA] 2011). Additionally, the fetch across open water to the shoreline at Rodanthe, Waves, and Salvo was greater (100 km) in the direction of the strongest winds (34 m/s, from the southwest) observed during Irene than the fetch to the other surveyed shorelines (Table 3.2, Fig. 3.4A) (NOAA 2011). Pre-hurricane structural condition of the bulkhead, wave exposure, fetch, and nearshore bathymetry presumably all contributed to observed differences in bulkhead performance among study regions during the hurricane.

Bulkheads were the only type of shoreline protection structure that showed visible damage after the hurricane (Fig. 3.4A). Thieler and Young (1991) also found greater damage to bulkheads when compared to riprap revetments along barrier island shorelines in South Carolina after Hurricane Hugo. They attributed the high rate of damage to bulkheads (58% of 6.1 km of bulkheading destroyed) and riprap revetments (24% of 7.1 km destroyed) to overtopping by the storm surge (Thieler and Young 1991). Most of the bulkhead failures observed in our study were probably also a consequence of overtopping of bulkheads by waves and storm surge (Table 3.2). Bulkheads retain landward sediment at an elevation 1-2 m higher than the natural shoreline. This large difference in elevation, when compared to typically lower-sloped marsh, riprap revetments, or sills, can result in a large and rapid loss of sediment if the stabilizing structure (the bulkhead) collapses or is breached(Fig. 3.3D). This process was evident from the large amount of sediment lost at all collapsed bulkheads surveyed throughout the NC coast (Fig. 3.4B). Damage to bulkheads was frequently observed directly adjacent or close to shorelines stabilized with riprap revetments, hybrid structures, and sills that were not damaged (R.K. Gittman personal observation), even along the Rodanthe, Waves, and Salvo shorelines. One of the sill sites surveyed on Bogue Banks was located approximately 100 meters from a collapsed bulkhead and experienced no change in overall marsh elevation in 2011 (Fig. 3.3D and 3.5A).

To evaluate the generality of some of our findings, our post-Irene results can be compared to those presented by Currin and colleagues (2007), who evaluated shoreline erosion in Bogue Sound after Hurricane Isabel. Specifically, Irene-induced changes in marsh surface elevation at the western-most marsh with sill and marsh without sill sites from before to after

Hurricane Irene in PKS, NC (Fig. 3.2E) can be compared to changes observed by Currin et al. (2007) at the same sites from before (spring 2003) to after (spring 2004) Hurricane Isabel (Category 2 at landfall, 45 km to the northeast of these two sites, Table 3.2). Marsh surface elevation increased 23.96±2.60 (SE) cm in the marsh with a sill and 11.87±2.53 (SE) cm in the marsh without a sill following Hurricane Isabel, whereas no significant change in surface elevation was observed following Hurricane Irene (Fig. 3.5A). Currin et al. (2007) also found an increase in marsh elevation after Isabel at two additional marshes with sills and two marshes without sills along shorelines of Bogue and Core Sound, NC. The increases in surface elevation after Isabel, as contrasted to the absence of change in surface elevation after Irene, may have been caused by transport of sediment during the longer period of sustained high winds and the wind direction with maximum gusts coming from the north (perpendicular to the shoreline) during Isabel (Table 3.2). Storm winds from the north would have increased wave heights at these north-facing study sites, potentially increasing sediment transport and deposition onto the marsh.

The immediate loss of marsh vegetation after Hurricane Irene followed by subsequent recovery of vegetation density within 13 months indicates that the impacts of Hurricane Irene on marsh vegetation at sill and unmodified sites on Bogue Banks were temporary. However, a non-significant difference was also observed in the amount of recovery of the marsh between sill and unmodified sites, with vegetation density at sill sites recovering more completely within the year than at unmodified sites (Fig. 3.5B). This potential difference in vegetation recovery between sill and unmodified sites could be explained by the ability of sills to protect the marsh by acting as a breakwater, much like an intertidal oyster reef would function, allowing lost or damaged vegetation to regrow in a more sheltered setting, thus potentially enhancing marsh recovery

(Meyer and Townsend 1997). Currin et al. (2007) found an increase in vegetation density at all sites during the year following Hurricane Isabel. Because neither hurricane resulted in surface elevation or permanent vegetation loss, it appears that marshes both with and without sills provided erosion protection during each storm event.

Marshes with and without sills presumably provided erosion protection via wave attenuation and stabilization of sediments (Shepard et al. 2011). Shepard and colleagues conducted a meta-analysis on the protective role of coastal marshes and evaluated the ability of marshes to perform the following functions: wave attenuation, sediment stabilization, and floodwater attenuation. Positive correlations between marsh width and wave attenuation and marsh width and sediment stabilization were found. Additionally, the meta-analysis revealed that marshes less than 10 m in width (which is the width of many fringing marshes found along the NC shorelines surveyed in our study), can reduce wave heights by 80% for waves < 0.5m in height and can reduce wave heights by 50% for waves > 0.5m in height. In terms of sediment stabilization, marshes promoted vertical sediment accretion, reduced sediment loss, and maintained or increased the surface elevation of the shoreline. We acknowledge that wave attenuation abilities of marshes decreases with increasing wave height and because water levels exceeded 0.5 m at our study regions (see Table 3.2), wave attenuation was likely less than 50% for marsh shorelines in this study. However, given the lack of visible damage and change in surface elevation or vegetation density in comparison to the damage observed to bulkheads within our study regions, we conclude that sills and marsh vegetation stabilized the shoreline despite reduced wave attenuation capabilities of marshes during the storm.

Although marshes with sills sustained little damage as a result of Hurricane Irene, data on the long-term performance of these structures are still necessary to determine their viability as

shoreline protection structures. Bulkheads and riprap revetments are estimated to have an average lifespan of 30 years and 50 years, respectively, with appropriate maintenance required, particularly for bulkheads (NC DCM 2011). However, bulkhead maintenance often includes back filling of landward sediment that has been lost over time to "hold the line" against erosion. The lifespan of marshes with sills is less certain because a majority of the existing sills in NC was constructed within the last 20 years (Fear and Bendell 2011). However, an assessment by NC DCM in 2011 revealed that all sills constructed in North Carolina remained intact and most of the sills were preventing erosion of the shoreline (Fear and Bendell 2011). Occasional supplemental planting of the marsh is the only maintenance described by property owners with sills (L. Weaver, *personal communication*). Long-term measurements (decades) of changes in marsh surface elevation and vegetation density at sites with sills, as well as measurements during larger storms, are necessary to truly determine the lifespan of this type of shoreline protection. *Research framework for informing shoreline protection decisions*

This study provides much needed data on the shoreline protection capabilities of different shoreline protection approaches that will help inform coastal management policies. However, data on the performance of shoreline structures during multiple storm events over a wider geographic area, cost efficiency, ecological effects, and the reversibility and adaptability of shoreline protection approaches with climate change are needed for waterfront property owners and coastal mangers to make truly informed decisions about shoreline protection. Here we present a framework for fulfilling the remaining data needs on shoreline protection.

The observed performance of shore protection structures may be limited to the geographic region and to the size and characteristics of the specific storm evaluated in this study. Additional studies evaluating the performance of shore protection in different geographic regions

during storms of different magnitudes, durations, and physical characteristics are needed. Data on the age and condition of shore protection structures prior to storm events should also be collected whenever possible. Finally comparisons of shore protection performance within the same geographic region across multiple storm events would also contribute to a more comprehensive understanding of the relative performance of estuarine shore protection structures.

The cost of installing a shoreline protection structure can be a key consideration for a coastal property owner deciding how to protect his or her shoreline. In North Carolina, the average construction cost in 2011 of bulkheads and riprap revetments was estimated to be \$450 per linear meter and \$400 per linear meter, respectively, with a combination costing approximately \$850 (NC DCM 2011). Marsh planting was estimated to cost \$70 per linear meter (assuming a 6 m-wide marsh) and construction of a granite marsh sill (including marsh planting) was estimated at \$500 per linear meter (NC DCM 2011). Although the average construction costs for bulkheads, riprap revetments, and marsh sills are similar, the replacement cost of marsh sills and riprap revetments is likely much lower than the initial construction costs, because the rock structure would likely only need to be rearranged or augmented rather than replaced entirely in the event of structure failures (FitzGerald et al. 1994, Thieler and Young 1991). Given the documented poor performance of bulkheads relative to riprap revetments and marshes with and without sills in this study, bulkheads are probably the least cost effective method for shoreline protection. However, cost effectiveness needs to be further evaluated to include maintenance and replacement costs as a function of inflating materials and labor costs and the availability of qualified contractors for different shoreline protection approaches.

In addition to considering the engineering capability and cost efficiency of a shoreline protection approach, policymakers should consider the effects of each shoreline protection approach on the ecosystem services provided by marsh and the broader coastal ecosystem. Bulkheads can cause deepening of adjacent shallow subtidal waters via wave refraction and scour, resulting in loss of marsh and seagrass habitat (NRC, 2007). Bulkheads are generally associated with reduced abundances of upland coastal marsh plant species, fish and crustaceans, and benthic infauna (Bilkovic and Roggero 2008, Bozek and Burdick 2005, Seitz et al. 2006). Riprap revetments are associated with higher fish and crustacean abundance and diversity than bulkheads, but not natural marshes, probably because riprap provides more structurally complex habitat than a vertical bulkhead wall, but not necessarily more complex than natural marshes (Bilkovic and Roggero 2008, Seitz et al. 2006). In contrast to bulkheads and riprap revetments, sills create sheltered habitat suitable for coastal marsh and seagrass plants and sills are associated with higher fish and crustaceans abundances equivalent to abundances found in natural marshes (Currin et al. 2007, Chapter 4: Gittman et al. in review, Hardaway et al. 2002, Scyphers et al. 2011, Smith et al. 2009). Nevertheless, relevant data are limited, so additional multi-year, multisite, and before-after-control-impact studies are needed to determine the net ecological effects of each alternative shoreline protection approach (NRC 2007).

As sea levels continue to rise, bulkheads and riprap revetments will inhibit transgression as the lower edge of the marsh progressively erodes, resulting in net loss and ultimately disappearance of the marsh habitat (Peterson et al. 2008a,b,Titus 1998).This loss of habitat should result in violation of Section 404 of CWA, implying that the USACE may need to consider how to require mitigation for these losses. Based on the physical characteristics described above and the costs provided in this section, reversing marsh habitat loss associated

with a bulkhead by removing the bulkhead and restoring lost coastal marsh by replanting would be more arduous and costly than supplemental marsh planting or moving or reinforcing a sill. However, research is needed on the feasibility of removing or adaptively managing and modifying alternative shoreline protection structures already in place.

Conclusions

This study contributes important information on the shoreline protection capabilities of several shoreline protection approaches and is the first study to contrast the performance of bulkheads and riprap revetments to marsh plantings with and without sills during a major storm. Additionally, a framework is provided for future research on the long-term shoreline protection capabilities, cost effectiveness, ecological effects, and reversibility and adaptability of shoreline protection structures. Scientists should focus on filling data gaps, particularly by evaluating the performance of shore protection structures in multiple storm events and by quantifying the ecological effects of alternative shoreline protection approaches. Policymakers should consider data from each component of this decision-framework to develop a synthetic set of policies related to estuarine shoreline protection.

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TABLES

 Table 3.1. Mixed model results for erosion analysis of marshes with sills and without sills

Response Variable	Fixed Factors	DF	F Ratio	Prob > F	REML Variance Component Estimates	Var Ratio	Var Component	Std Error	95% Cl Lower	95% Cl Upper	Percent of Total
	Shoreline type (sill or no sill)	1	14.60	0.001	Site	0.254	0.004	0.002	0.000	0.008	20.25
	Year (2010, 2011, 2012)	2	0.07	0.930	Residual		0.016	0.002	0.013	0.020	79.75
Marsh	Plot (distance from marsh edge)	4	59.20	<.0001	Total		0.020	0.002 0.016 0.026	0.026	100.00	
surface elevation (m)	Shoreline type*Year	2	0.01	0.992							
	Shoreline type*Plot	4	7.20	0.000							
	Plot*Year	8	0.19	0.990							
	Shoreline type*Plot*Year	8	0.21	0.988							
	Shoreline type (sill or no sill)	1	3.27	0.078	Site	0.536	882	307	280	1484	34.88
	Year (2010, 2011, 2012)	4	4.12	0.007	Residual		1647	167	1362	2031	65.12
Marsh stem density per m ²	Plot (distance from marsh edge)	2	4.62	0.015	Total		2529	321	2001	3297	100.00
	Shoreline type*Year	2	1.28	0.289							
	Shoreline type*Plot	4	0.34	0.846							
	Plot*Year	8	0.79	0.611							
	Shoreline type*Plot*Year	8	0.10	0.999							

Table 3.2. Meteorological and water level data for surveyed locations during Hurricane Irene and Hurricane Isabel.

	Rodanthe, Waves, & Salvo ^ª	Frisco & Hatteras Island ^b	Bogue Banks ^c		
Hurricane parameter	Irene	Irene	Irene	Isabel	
Duration at or above Tropical Depression speed	30 hours	24 hours	29 hours	38 hours	
Average wind speed	17 m/s	12 m/s	22 m/s	17 m/s	
Maximum gust	34 m/s	32 m/s	35 m/s	40 m/s	
Maximum gust direction	Southwest	East	East northeast	North	
Max fetch from max gust direction	100 km	4 km	5 km	5 km	
Storm tide	2.32 m	1.25 m	1.91 m	1.61 m	
Predicted tide	0.16 m	0.13 m	0.99 m	0.74 m	
Storm surge/residual	2.16 m	1.12 m	0.92 m	0.87 m	

^a Data collected from the Oregon Inlet station (ORIN7 8652587), NOAA National Data Buoy Center and the NOAA tide station at the Oregon Inlet Marina, NC (8652587) from August 26, 2011 to August 28, 2011.

^b Data collected from the Cedar Island station (NCDI), State Climate Office of North Carolina and from the NOAA tide station at the US Coast Guard Station Hatteras, NC, from August 26, 2011 to August 28, 2011. NCDI was the closest wind station available because the Hatteras Island wind station was damaged during the hurricane.

^c Data collected from the Cape Lookout station (CLKN7) and the NOAA tide station at the NOAA Beaufort Lab, Beaufort, NC, from September 17, 2003 to September 19,2003 and August 26, 2011 to August 28, 2011.

FIGURES



Figure 3.1. Photographs of shoreline types: a) a bulkhead: a vertical structure typically constructed of vinyl composite, concrete, asbestos, or treated wood placed at or above the observed high water mark; b) a riprap revetment: a sloped structure typically constructed of granite, marl, or concrete placed at or above OHWM; and c) a sill: a structure typically constructed of granite, marl, or oyster shell, seaward of marsh.

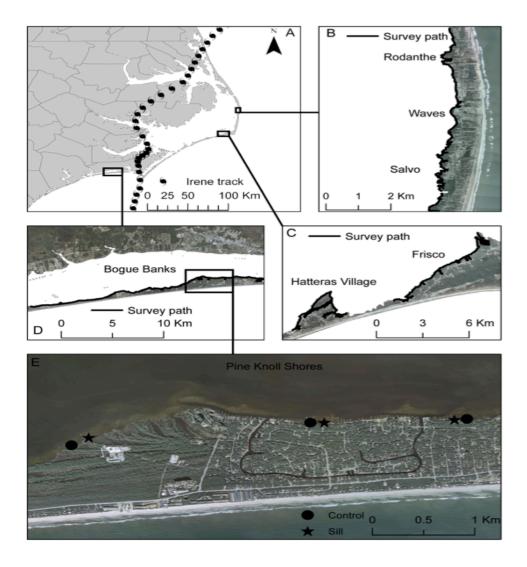


Figure 3.2. A map of: a) the study areas relative to the path of Hurricane Irene (made landfall in NC at 34.7°N, 76.6°W; b) survey path for damage classifications on Rodanthe, Waves, and Salvo, NC; c) survey path for damage classifications on Frisco and Hatteras Island, NC; d) survey path for damage classifications on Bogue Banks, NC; and e) zoom-in to the sill sites and unmodified marsh sites that were surveyed along Bogue Banks, NC. The Hurricane Irene track and rate of movement is depicted at 30-minute intervals by the location symbol.



Figure 3.3. Bulkhead damage classifications: a) Landward erosion; b) Structural damage: c) Breach; and d) Collapse.

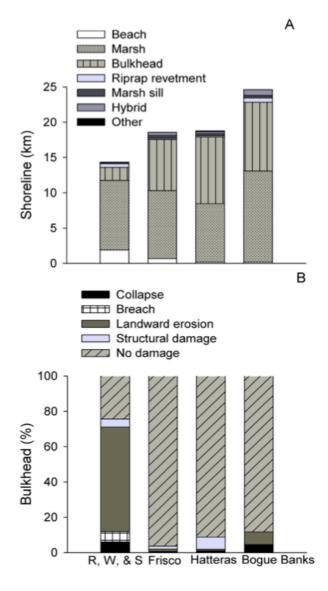


Figure 3.4. a) Shoreline classification by type (km) for Rodanthe, Waves, and Salvo; Frisco; Hatteras Village; and Bogue Banks, NC. *See* Fig. 1 for descriptions and photographs of a bulkhead, riprap revetment, and marsh with a sill. Hybrid is a combination of bulkhead and riprap and beach is unvegetated shoreline. b) Bulkhead damage classification by type (%) for Rodanthe, Waves, and Salvo (R, W, & S); Frisco; Hatteras Village; and Bogue Banks, NC. *See* Fig. 3 for photographs of damage classifications.

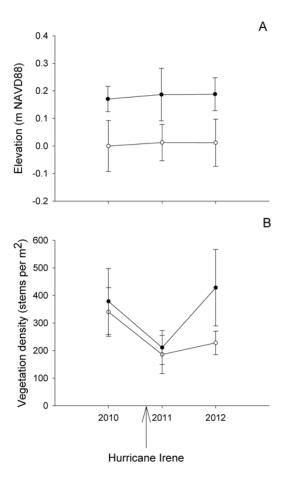


Figure 3.5. The effects of Hurricane Irene on: (a) average marsh surface elevation (m, NAVD88); and (b) average vegetation density per m^2 at marsh sites with (closed circles) and without (open circles) sills. Error bars represent $\pm 1SE$ (n=9 to 21 per site).

CHAPTER 4: LIVING SHORELINES CAN ENHANCE THE BIOGENIC STRUCTURE AND NURSERY ROLE OF THREATENED ESTUARINE HABITATS

Abstract

Coastal ecosystems provide numerous services, such as nutrient cycling, climate change amelioration, and habitat provision for commercially valuable organisms. Ecosystem functions and processes are modified by human activities locally and globally, with degradation of coastal ecosystems by development and climate change occurring at unprecedented rates. Paradoxically, the demand for coastal defense strategies against storms and sea-level rise has increased with human population growth and development along coastlines worldwide, even while that population growth has reduced natural buffering of shorelines. Shoreline hardening, a common coastal defense strategy that includes the use of seawalls and bulkheads (vertical walls constructed of concrete, wood, vinyl, or steel), is resulting in a "coastal squeeze" on estuarine habitats. In contrast to hardening, living shorelines, which range from vegetation plantings to a combination of hard structures and plantings, are often deployed to restore or enhance multiple ecosystem services normally delivered by naturally vegetated shores. Although hundreds of living shoreline projects have been implemented in the U.S. alone, few studies have evaluated their effectiveness in sustaining or enhancing ecosystem services relative to naturally vegetated shorelines and hardened shorelines. We quantified the effectiveness of (1) sills with landward marsh (a type of living shoreline that combines marsh plantings with an offshore low-profile breakwater), (2) natural, salt marsh shorelines (control marshes), and (3) unvegetated bulkheaded shores in providing habitat for fish and crustaceans (nekton). Sills supported higher abundances

and species diversity of nekton than unvegetated habitat adjacent to bulkheads and even control marshes. Sills supported higher cover of filter-feeding bivalves (a food resource and refuge habitat for nekton) than bulkheads or control marshes. This ecosystem-service enhancement was detected on shores with sills three or more years after construction, but not before. Sills provide added structure and may provide better refuges from predation and greater opportunity to use available food resources for nekton than unvegetated bulkheaded shores or control marshes. Our study shows that unlike complete shoreline hardening, living shorelines can enhance some ecosystem services provided by marshes, such as serving as nursery habitat.

Introduction

Interdisciplinary studies between ecologists and economists have resulted in major advances in the valuation of services provided by ecosystems in the past two decades (Millennium Ecosystem Assessment [MEA] 2005, Naidoo et al. 2008, Carpenter et al. 2009). Ecosystem services are the direct and indirect benefits that humans derive from ecosystems, and include, nutrient cycling, climate regulation, habitat provision for organisms of value, and recreational uses (Carpenter et al. 2009). Many human activities are degrading coastal ecosystems and the services they provide (Vitousek et al. 1997, MEA 2005, Dahl and Stedman 2013). Coastal development and global climate change, particularly sea-level rise and increased storminess, are threatening coastal ecosystems and have already resulted in significant losses of these ecosystems (MEA 2005, Hoegh-Guldberg and Bruno 2010). With over 123 million people living within 100 km of a U.S. coastline (U.S. Census Bureau 2010), there is considerable need for development strategies that sustain, restore, or enhance delivery of ecosystem services.

One of the most pressing concerns over continued coastal development is protection against erosion and subsequent property loss resulting from the joint impacts of storm events and sea-level rise (Törnqvist and Meffert 2008, Temmerman et al. 2013). Traditional shoreline protection methods, such as seawalls or bulkheads, are designed to protect the shore from erosion and public or private infrastructure from flood and structural damage, but can fail during major storm events and even exacerbate impacts (Thieler and Young 1991, Chapter 3: Gittman et al. 2014). In contrast to the erosion and damage protection provided to upland property, these structures can induce erosion of habitats located seaward of or adjacent to the structure, resulting in the loss of valuable intertidal and/or shallow vegetated, beach, or mudflat habitat (Hall and Pilkey 1991, Doody 2004, Bozek and Burdick 2005, Dugan et al. 2008, Pontee 2013). Further, as sea levels rise, a "coastal squeeze" can occur where coastal habitat is lost from the high water mark being fixed by a structure and the low water mark migrating landward as sea level rises (Titus 1998, Peterson et al. 2008, Pontee 2013). Additionally, bulkheads and seawalls support a lower abundance and diversity of benthic infauna, fish, and mobile crustaceans than natural shorelines dominated by salt marsh (Bilkovic and Roggero 2008, Dugan et al. 2008, Lucrezi et al. 2010, Seitz et al. 2006). Heightened awareness of the adverse ecological effects of "hard" shoreline protection methods and the billions of dollars in damage done to coastal properties and infrastructure by major storm events (e.g., Hurricane Katrina in 2005 and Superstorm Sandy in 2012 in the U.S.) has increased demand for alternative effective methods that incorporate natural components for coastal protection (Arkema et al. 2013, Cheong et al. 2013).

Some alternative methods of coastal protection, broadly termed "living shorelines", include restoration of habitats that provide natural protection from erosion, such as salt marshes and intertidal oyster reefs (Crooks and Turner 1999, Piazza et al. 2005). Living shorelines also

include hybrid techniques, that consist of pairing an offshore sill composed of granite boulders, concrete, marl, or oyster shell with marsh plantings (referred to as sill hereafter, *see* Figure 1 for examples of sills, NRC 2007, Currin et al. 2009). Over 200 projects identified as "living shorelines" have been permitted and constructed in the U. S., with marsh sills comprising more than half of them (Fear and Bendell 2011, Coasts, Oceans, Ports, and Rivers Institute [COPRI] 2014, Chesapeake Bay Trust 2014). The goals of these projects are to go beyond providing erosion protection to include sustaining additional ecosystem services, such as provision of habitat for various marine organisms and filtration of nutrients or pollutants (COPRI 2014). However, few studies have assessed the success of living shoreline approaches in sustaining or enhancing ecosystem services (but *see* Currin et al. 2007, Scyphers et al. 2011, La Peyre et al. 2014). Furthermore, existing studies have only evaluated the short-term ecological functions of living shorelines (< three years post-construction) and have not included comparisons to the ecological functions of bulkheaded shores.

We hypothesized that hybrid living shorelines, sills with landward marsh, would support higher abundances, biomass, and diversity of mobile fishes and crustaceans (nekton), particularly juveniles and estuarine residents, than fringing salt marshes alone or than unvegetated bulkheads. Our hypothesis is based on the expectation that sills would enhance pre-existing uses of habitat through one or both of the following mechanisms: (1) increasing the structural complexity of the habitat and providing spatial refuge from predation and environmental stress (i.e., wave exposure); and (2) increasing resource (food) availability via providing additional substrata for epibiota (prey) and organic matter deposition. Nekton abundance and production are positively related to structural habitat complexity, such as submerged aquatic vegetation (Orth et al. 1984, Bell and Westoby 1986), oyster reefs (Grabowski and Peterson 2007, Grabowski et al. 2008,

Stunz et al. 2010), and salt marshes (Peterson and Turner 1994, Minello et al. 2003) relative to mudflat or sandy bottom habitats, which lack emergent structure. The addition of substrate may also increase the availability of epibiota (e.g., oysters, mussels) and other organic materials as food resources (Peterson et al. 2003). To test our hypothesis, we compared nekton catch rates and diversity along sills of varying ages (zero to eight years) to shorelines with natural, fringing salt marshes, and to bulkheaded shorelines without marsh.

Methods

Study Design

To ensure that our study would provide a comprehensive assessment of nekton use of habitats associated with different shore stabilization approaches, we made four independent comparisons of nekton catch rates along different types of shorelines. We first compared nekton catch rates and diversity in intertidal marsh (Figure 4.A-1A) and shallow subtidal habitat (Figure 4.A-1B) between sites with sills (three or more years after sill construction) and sites without sills (control marsh sites), referred to as the control-impact (CI) study. We also compared nekton catch rates and diversity in intertidal marsh and shallow subtidal habitat before and after sill construction to nekton catch rates and diversity at control sites, referred to as the before-after-control-impact (BACI) study. We then determined if nekton catch rates and diversity in habitat adjacent to sills differed between a newly constructed sill and sills that had been in place for three or more years (the period of time estimated to be necessary for nekton catch rates and diversity at a BACI sill less than one year after construction and at three CI sill sites (one sill three years and two sills eight years after construction) within the same geographic region.

Finally, we compared nekton catch rates and diversity in unvegetated intertidal habitat adjacent to sills, adjacent to bulkheads with no marsh, and adjacent to control marsh sites (Figure 4.A1-C), referred to as bulkhead comparison (BC) study. To identify factors (e.g., increased structural complexity) potentially associated with differences in nekton catch rates and diversity among different shoreline types, we also measured habitat characteristics (see below) at each shoreline type.

Description of study sites

The CI study consisted of surveying three existing granite sills and three control marsh sites located in Pine Knoll Shores (PKS), NC (Figure 4.1A, 34°42'11"N, 76°48'21"W). At each sill site, a sill consisting of piled granite boulders (20-cm to 50-cm diameter) was constructed between the years of 2002 and 2007 (Figure 4.1E). The elevation of the base of each sill was between 0.14 and 0.31 m below mean sea level (MSL). Each sill had an average height ranging from 0.2 m (base to top of the sill) for the oldest sill to 0.56 m for the youngest sill. Each sill also had either a drop-down (area of lower elevation interrupting the sill crest, Figure 4.A-2A) or a gap (a break in two sill sections, Figure 4.A-2B) to allow water to flow behind the sill at intervals of approximately every 20 m for the entire length of the sill (range: 40 - 100 m long). Marsh grasses, Spartina alterniflora and S. patens, were planted behind each sill along the lower edge of existing high marsh at elevations consistent with the positions of these two grasses in nearby unmodified marshes (Currin et al. 2007, J. Shallcross and J. Best personal communications). To minimize site-specific differences that may affect nekton catch rates, we paired each sill site to a control site with similar physical characteristics (e.g., marsh width, wave exposure) and close proximity (<200 m) along the same shoreline (Figure 4.1F).

BACI sites were located in PKS, NC, Hatteras, NC (35°13'18"N, 75°41'35"W),

Swansboro, NC (34°41'49"N, 77° 6'24"W), and Holly Ridge, NC (34°28'12"N, 77°30'28"W) (Figure 4.1A). At each site, a low sill, consisting of granite boulders (Hatteras and PKS, Figure 4.1B and C) or oyster shell bags (Holly Ridge and Swansboro, Figure 4.1G and H), was constructed to a height just above MSL. Each sill had an average height ranging from 0.3 m (oysterbag sills) to 0.7 m (stone sills). As with our CI sites, *S. alterniflora* (low marsh) and *S. patens* (high marsh) were planted behind the sill at elevations consistent with nearby marshes. The Swansboro, Hatteras, Holly Ridge, and PKS sills were constructed in September 2010, March 2011, November 2011, and April 2012, respectively. The Swansboro and Hatteras sill sites were planted in May 2011 and the Holly Ridge sill site was planted in May 2012. The PKS sill site was not planted during the study period. A marsh control site was selected as described above for CI sites. The PKS sill site from this BACI study was also compared to the CI study sill sites to test for the effects of sill age on ecosystem service delivery (nekton use).

For the BC study, we selected three bulkheaded sites with no seaward marsh in PKS along the same shoreline as the CI sills and control marshes (Figure 4.1D-F). Each bulkhead consisted of a vertical vinyl wall constructed at the Observed High Water Mark (OHWM) or approximately 0.59 m above MSL (NOAA 2014).

Nekton sampling

We conducted all nekton sampling monthly from June to October, with CI, BACI, and BC sampling occurring in 2010, from 2010 to 2012, and in 2011, respectively. We sampled nekton utilizing the marsh (defined here to include the marsh interior, marsh edge, and unvegetated mudflat within 3 m of the marsh edge) at paired sill and control marsh sites (CI study) by simultaneously setting two fyke nets at each site during a night spring high tide and

recovering gear during the subsequent low tide (\sim 6-hr sets, Figure 4.A-1A). Fyke nets were placed at the sill drop-downs or gaps at the sill sites (Figure 4.A-3) and randomly along the edge of control marsh sites. Fyke net openings were set at approximately the same distance from the marsh edge (3 - 5 m, depending on sill location relative to the marsh edge) at each paired site (Rozas and Minello 1997, Currin et al. 2007). The fyke nets consisted of a 0.9-m by 0.9-m by 5.1-m compartmentalized, 3.175-mm-mesh-net bag with 0.9-m by 5.1-m wings that stretched out from the bag (set for a total mouth width of 8 m). To determine nekton catch rates and diversity of subtidal habitats adjacent to sills and at control sites (CI study), we seined two times parallel to the shoreline for 20 m (approximately 5 m from the sill or marsh edge) at each site during afternoon spring low tides (Figure 4.A-1B). Seines were 7.3 m wide by 1.8 m tall, made from 3.175-mm-mesh net, and included a 1.8-m by 1.8-m by 1.2-m bag. Nekton use of unvegetated subtidal habitat within 1 m of sills (between the sills and landward marsh edges), and seaward of bulkheads and control marshes was assessed by setting replicate (n=10) minnow traps (3.175mm-galvanized mesh) at the edge of each shoreline type two hours before high tide and collecting the traps two hours after high tide (Figure 4.A-1C).

Nekton was identified to species, when possible, counted, and weighed wet, before the first twenty of each species were measured for standard length (fish and shrimp) or carapace length (crabs) either in the field or in the lab (after being held or transported using buckets and air bubblers), with subsequent release. All species were classified as resident or transient and the mean length and biomass data were used to determine if a majority of individuals were juveniles or adults for each species, as per Hettler (1989) and Peterson and Turner (1994). We pooled across nets or traps at each site and abundance data are reported as catch per unit effort (CPUE) for nekton caught by all nets or traps per site per sampling effort (individuals or grams per set).

Sampling effort was standardized as two fyke nets soaking for six hours, two 20-m seine pulls, and ten traps soaking for four hours.

Habitat characteristics

We measured several habitat characteristics (e.g., marsh surface elevation, marsh macrophyte density, sediment organic matter [SOM] content) to better assess the relationship between shoreline type and nekton use of available habitats. To characterize the intertidal habitat structure available to nekton, we quantified total stem density of marsh macrophytes at each CI and BACI site. Five intertidal transect locations were selected using restricted random (between 10 m and 20 m apart to maintain independence) sampling (Neckles et al. 2002). Transects began at the seaward edge of the marsh and continued to the start of shrub-scrub vegetation or to property-owner landscaping. Marsh plots were established at 3- or 5-m intervals along each transect beginning at the lower marsh edge. The length of each transect (5 - 20 m) and total number of marsh plots established (9-21) depended on the marsh width from seaward edge to upland vegetation at each site. Stem density was measured by marsh plant species per 0.25-m² plot (Daoust and Childers 1998). Total stem density of marsh plants was calculated by summing the stem densities of all species present within a plot. We surveyed subtidal areas up to 20 m seaward of the marsh edge to determine the type of subtidal habitat available to nekton at all CI and BACI sites (e.g., sand/mud flat, seagrass, or both). Sampling plots began at the lower marsh edge and seagrass shoot density was estimated every 5 m along each transect by counting the total number of shoots per species inside 0.25-m² guadrats (Hauxwell et al. 2001).

Surface elevation was measured within 1 m landward of the sill using a leveling rod and rotary laser level and referencing the measurements to semi-permanent benchmarks (points established on a stable structure with unchanging elevation, e.g., a piling or tree) with elevations

determined using a Trimble Virtual Reference Station (VRS), Real Time Kinematic (RTK), Global Positioning System (GPS). North American Vertical Datum of 1988 (NAVD88) elevations obtained using these methods are estimated to be accurate to \pm 6 cm (P. Hensel *personal communication*). To determine the availability of organic material available to benthic or filter-feeding nekton, we took sediment organic matter (SOM) samples by coring the top 3-5 cm of sediment at every plot on all site transects. Cores were transported to the lab and frozen for later analysis. For SOM analysis, a homogenized subsample of approximately 30 g (wet weight) was dried overnight at 100°C, weighed, and then ashed at 450°C for 6 – 8 h and reweighed to obtain ash-free dry weight by subtraction (Currin et al. 2007). To determine availability of epibiota (macroalgae and invertebrates) at sill, control marsh and bulkhead sites, we sampled the sills (granite), control marsh edges (unconsolidated sediment), and bulkheads (vinyl) in September 2011. We determined the percent cover and species composition of epibiotic species attached to the substrate using the point-intersect method, with 16 intersections within a 0.25-m² quadrat.

Statistical analyses

Because of natural environmental variability among our sites (e.g., proximity to channels, shoreline orientation, sample date), we paired our CI sill and control marsh sites for all analyses. We compared catch rates and Shannon-Wiener diversity indices (H') of nekton between paired CI sill sites and control marsh sites using grouped (by site), matched pairs two-tailed t-tests. Catch rates of nekton were analyzed separately for each habitat (marsh samples using fyke nets or subtidal samples using seines). We also compared the mean total stem density (m⁻²) of marsh plants, sediment surface elevation 1-m landward of the sill, and SOM (%) using matched pairs two-tailed t-tests.

function of distance from the marsh edge, we compared mean total shoot density (m⁻²) of all seagrasses as a function of distance from the marsh edge (1, 5, 10, 15, and 20 m) at sill and control sites using a one-factor (sill vs. control) repeated measures analysis of variance (ANOVA), with distance from marsh edge as the repeated measure.

To compare the catch rates of nekton between BACI sill sites and control marsh sites before and after the sills were constructed, we performed separate BACI analyses (two-way ANOVAs) for each site, with treatment (sill vs. control marsh), time (before vs. after), and treatment by time as fixed factors.

We compared the mean differences in catch rates of nekton between the three CI sills and control marsh sites in PKS to the mean difference between the BACI sill (less than one year post-construction) and control marsh in PKS site using a one-sample t-test (transforming all sillminus-control data so that BACI differences would equal 0). We also compared the mean surface elevation 1-m landward of the sill, SOM, and stem density of marsh macrophytes between each CI sill and the BACI sill using a one-sample t-test.

We compared catch rates of nekton between sill, control marsh, and bulkhead-with-nomarsh sites using nested ANOVAs with treatment (sill vs. control vs. bulkhead) as a fixed factor and sampling month nested within each site. We preferred a nested ANOVA over the matched paired analysis used to compare the sills and control marsh sites alone because unvegetated bulkhead sites could not be appropriately paired geographically to the sill and control marsh sites.

Catch rates, density of marsh plants, and shoot density of seagrass were log-transformed prior to analysis to meet the assumptions of normality (Shapiro-Wilk Test, P > 0.05) and homogeneity of variance (Levene's test, P > 0.05). Because we applied each statistical test to

separate, pre-defined hypotheses, an alpha level of 0.05 was used for all hypothesis testing. (Hurlbert and Lombardi 2003, Moran 2003). Analyses were conducted using JMP 10.0 (SAS 2012).

Permutational analysis of variance (PERMANOVAs) on the Bray-Curtis similarity matrices of nekton communities were performed to uncover any significant community differences in each habitat between individually paired CI and BACI sill and control marsh sites. Nekton species abundances were fourth-root transformed to reduce the effect of the most abundant species when testing for differences in community composition. Species that were present only in a single sample were excluded from the analyses. We used non-metric multidimensional scaling (NMS) and similarity percentages (SIMPER) to assist with interpretation of differences in nekton community structure between sill and control marsh sites. PERMANOVAs on the Euclidean distance matrices of barnacle, bivalve, and other epibiota were performed separately to decipher significant differences in epibiota on sills, bulkheads, and control marshes. Permutational Dispersion (PERMDISP) was used to test for homogeneity of variances. As with univariate testing, an alpha level of 0.05 was used for all multivariate hypothesis testing. Multivariate analyses were conducted using PRIMER-E software 6.1.1 with PERMANOVA+ 1.0.1 (Clarke and Gorley 2001).

Results

CI comparison

We found higher catch rates of fishes within the marsh at sill sites than at control sites (Figure 4.2A, individuals per 2 fyke net sets, t-ratio= -4.61, DF = 14, P > |t| = 0.0004, and Figure 4.2B, grams per 2 fyke net sets, t-ratio= -3.44, DF = 14, P > |t| = 0.004). For crustaceans, we also

caught more individuals per 2 fyke net sets within the marsh at sill sites than at control sites (Figure 4.2A, t-ratio= -4.13, DF = 14, P > |t| = 0.001), but differences in crustacean grams per 2 fyke net sets were non-significant between sill and control sites (Figure 4.2B, t-ratio = -1.83, DF = 14, P > |t| = 0.08). Nekton community composition differed between two of the three pairs of sill sites and control marsh sites, with differences in community composition driven by higher catch rates of the most abundant nekton species (see below) in the marsh at sill sites (P < 0.05, Tables 4.1 and 4.B1). The diversity (H') of fishes within the marsh (2 fyke net sets) at sill sites was greater than at control sites (t-ratio= -3.83, DF = 14, P > |t| = 0.002).

Transient fishes such as mullets (*Mugil* spp.), pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), mojarra (*Eucinostomus* spp.), flounders (*Paralichthys* spp.), speckled trout (*Cynoscion nebulosus*), pigfish (*Orthopristis chrysoptera*), and silver perch (*Bairdiella chrysoura*), made up 93% of the individuals and 92% of the biomass caught within the marsh (fyke net catches) at sill sites and 97% of the individuals and 95% of the biomass caught at control marsh sites (Table 4.1). Marsh resident species, such as mummichogs (*Fundulus heteroclitus*), and striped killifish (*Fundulus majalis*), made up only 7% of the individuals and 8% of the biomass caught within the marsh at sill sites and only 3% of the individuals and 5% of the biomass caught at control marsh sites. Crustacean catches within the marsh at both sill and control sites consisted of shrimp (*Penaeid* spp. and *Palaemonetes* spp.) and crabs (primarily blue crab, *Callinectes sapidus*) (Table 4.1).

Catch rates, species diversity, and community composition of nekton using seagrass patches or mudflat adjacent to sills or control sites were not significantly different based on seine net sampling (Figure 4.2C-D, P > 0.1, Tables 4.B2 and 4.B3). *L. rhomboides* dominated seine

net catches at both sill and control sites, making up 77% and 82% of the individuals, respectively.

Mean total density of marsh macrophyte stems and mean SOM within the marsh did not differ between sill and control sites (Figure 4.3A-B, t-ratio = 0.78, DF = 2, P > |t| = 0.51 and t-ratio = -0.92, DF = 2, P > |t| = 0.46). Mean surface elevation (m) of the unvegetated area between the sill and the landward marsh edge was greater than the mean surface elevation within 1 m of marsh edge at control sites (Figure 4.3C, t-ratio = -6.16, DF = 2, P > |t| = 0.03). Mean total density of seagrass shoots did not differ between sill and control marsh sites (F = 0.19, DF = 1, P > F = 0.68), nor did density differ as function of distance from the marsh edge (F = 0.37, DF = 4, P > F = 0.83, Figure 4.3D).

BACI comparison

There was no effect of sill construction on nekton catch rates or community composition within intertidal (fyke net) or subtidal habitats (seine net) less than one year post-construction at any of the sampled BACI sites (Figure 4.4A-H, P > 0.1, treatment by time interaction, Tables 4.B4 and 4.B5).

CI and BACI sill comparison

The mean difference in fyke net catch rates of fishes within salt marsh habitat between older CI PKS sill sites (three to eight years post-construction) and paired control marsh sites was greater than the difference between fyke net catch rates at the BACI PKS sill site (less than one year post-construction) and paired control marsh site (Figure 4.5A, T = 14.4, DF = 2, P > |t| = 0.005). However, there was no analogous difference in crustacean fyke net catch rates (T = 2.7, DF = 2, P > |t| = 0.11). Only three of six resident species caught in fyke nets at the CI sill sites were caught at the BACI sill site (Table 4.1). Surface elevation (m) landward of the CI sills was

greater than surface elevation landward of the BACI sill (Figure 4.5B, T = 5.52, DF = 2, P > |t| = 0.03). SOM (%) landward of the CI sills was greater than SOM landward of the BACI sill (Figure 4.5C, T = 4.92, DF = 2, P > |t| = 0.04). Total stem density of marsh macrophytes was greater at CI sills than at the BACI sill; however, this difference was not significant (Figure 4.5D, T = 2.10, DF = 2, P > |t| = 0.17).

Comparison of sills, control marshes, and bulkheads

Catch rates (individuals and g per trap set) of fishes were greater along the unvegetated edge of sills than bulkheads (Figure 6A-B, P < 0.05, Tukey's posthoc tests, Table B6), while control marsh catch rates were not different from catch rates at marsh sill or bulkheaded sites (Figure 4.6A-B, P > 0.05, Tukey's post hoc tests). Trap catch rates of crustaceans were not different along the unvegetated edge between sill, control marsh, and bulkheaded sites (Figure 4.6A-B, individuals per trap set, F = 1.14, DF = 2, P = 0.38, and grams per trap set, F = 0.04, DF = 2, P = 0.95). Resident marsh fishes made up 81% of the individuals and 76% of the biomass caught in traps at sill sites, while marsh residents made up only 11% of the individuals and 15% of the biomass caught at control marsh sites, and were completely absent from unvegetated bulkheaded sites (Table 4.2). Epibiotic cover differed between sills, bulkheads, and along the edge of the control marshes (Figure 4.6C, Table 4.B7). The proportion of cover by filter-feeding bivalves (C. virginica and mytilid mussels) was greater on sills than on bulkheads or along control marsh edges (P < 0.05, PERMANOVA pair-wise tests). The proportion of cover by Semibalanus barnacles was greater on bulkheads than along control marsh edges (P < 0.05), but not different from sills (P > 0.05, PERMANOVA pair-wise tests). The proportion of cover by other epibiota (tunicates, sponges, and bryozoans) was greater on bulkheads than along control marsh edges and sills (P < 0.05, PERMANOVA pair-wise tests).

Discussion

Effects of sills on habitat use by fishes and crustaceans

Marshes with sills support higher abundances and diversity of nekton three or more years post-construction (Figure 4.2A-B and Figure 4.6A-B), but this enhancement is not evident immediately after construction (< one year) (Figure 4.5A-D). A majority of the transient species that we caught were juveniles (Table 1), indicating that the fringing salt marshes at our sites probably serve as nursery habitat (Hettler 1989, Minello et al. 2003, Peterson and Turner 1994). Marsh with sills may support higher abundances and diversity of nekton via multiple mechanisms: (1) Providing spatial refuges from predation for resident and juvenile fishes via increasing structural complexity of the habitat (Grabowski 2004); and (2) Increasing food availability via the colonization and growth of epibiota on the sill itself and accumulation of organic material (Bulleri and Chapman 2010, Craft 2003). Epibiota found on the sill (Figure 6C), such as oysters (Crassostrea virginica), mytilid mussels, Semibalanus barnacles, and bryazoans (Bugula spp.) occur naturally on intertidal oyster reefs (Wells 1961, Fodrie et al. 2014) and may serve as food for many of the fish and crustaceans we caught, including sheepshead (Archosargus probatocephalus), stone crabs (Menippe mercenaria), L. rhomboides and C. sapidus (Peterson et al. 2003). We found no evidence that SOM was enhanced by the presence of a sill (Figure 3B), rather SOM likely increased as a result of planting of marsh macrophytes landward of the sill. Therefore, the establishment of marsh seems necessary to provide SOM as a food source for juvenile and resident nekton.

Differences in nekton catch rates and diversity between 1-yr-old and 3-yr-old sills (Figure 4.5A) may be a consequence of any of several physical and biological differences in <1-yr-old

BACI and >3-yr-old CI sill sites. A lower mean surface elevation directly landward of the sill (-0.336 m NAVD88) at the PKS BACI sill site when compared to older PKS CI sill sites (-0.166 to 0.003 m NAVD88) meant greater water depths at high tide (Figure 4.5B). Deeper water facilitates more access of large predators to the marsh and thus potentially reduces (via predation or behavioral avoidance by prey) densities of juvenile fish and crustaceans found in the marsh. Ruiz et al. (1993) found that densities and survivorship of juvenile fishes and crustaceans increased with decreasing depth and most predators of these species were found at a depth over 0.7 m or greater. This depth is approximately the equivalent mean depth during high tide at an elevation of -0.2 m NAVD88 at our PKS study sites. Thus, the <1-yr-old PKS BACI sill had greater access for predators than the >3-yr-old PKS CI sills. The PKS BACI sill site also had a lower SOM content than the older PKS CI sill sites (Figure 4.5C), indicating that the PKS BACI sill provided less organic material and detritus for benthic-feeding species, such as *Mugil* spp. and *Palaemonetes* spp., to consume than the PKS CI sill sites. Fewer refuges from predation and lower food resource availability at the younger PKS BACI sill site as compared to the older PKS CI sill sites may have led to lower nekton abundances. This may be a consequence of the planted marsh, rather than the presence of the sill structure itself. Finally, the PKS BACI sill site tended to have lower total stem densities of all marsh macrophytes, and therefore lower structural complexity, when compared to the PKS CI sill sites (Figure 4.5D), although this difference was not statistically significant. Salt marsh macrophytes typically need multiple growing seasons to clonally expand and cover a site, and sediment surface elevation and SOM typically increase with salt marsh age, if sediment supply is adequate and subsidence is not occurring (Craft et al. 2002, 2003). We speculate that these results may indicate that the presence of a sill structure alone may not enhance nekton use of intertidal habitat and that marsh macrophyte establishment

(either through planting or natural recruitment) may be a critical aspect of enhanced of fish nursery habitat, although this hypothesis has yet to be tested.

We acknowledge that one of the shortcomings of control-impact designs is that observed differences between impact and control sites may be due to intrinsic differences in the sites, rather than differences caused by the "impact" of interest (Osenberg et al. 1994). However, as stated in the Methods, we have made efforts to minimize site-specific differences that may affect nekton catch rates. There are also potential concerns (e.g., differences in sites) with CI (sill post-construction versus control marsh) studies and with substituting space for time by comparing sill sites of varying ages to predict the trajectory of habitat development and nekton use of living shorelines. However, we used a combination of approaches (e.g., intensive sampling of nekton at multiple pairs of sill and control sites, measurements of multiple habitat characteristics) to evaluate the effects of living shorelines on nekton use. Despite these concerns, our results are consistent with the findings of other, complimentary studies (no enhancement of nekton 1-yr post-construction of sills, Currin et al. 2007, enhancement of nekton 2 to 3-yrs post-construction of oyster reefs, Scyphers et al. 2011 and Le Peyre et al. 2014).

In contrast to the observed enhancement of nekton abundances and diversity within the marsh at older sill sites (fyke net data), seine data suggest that the presence of a sill does not increase abundance or diversity of nekton within seaward seagrass or mudflat habitats, regardless of the age of the sill (Figure 4.2C-D, Figure 4.4E-H). Although not directly comparable due to different gear types being used for sampling, the nekton community occupying seagrass patches seaward of the sills was dominated by the same species that dominated the salt marsh catches (e.g., *Mugil* spp., *L. rhomboides*, *L. xanthurus*, *Eucinostomus* spp., and *Paralichthys* spp.), although *L. rhomboides* made up a larger percentage of the catches in seagrass. However, the

abundance and community composition did not differ between seagrass habitats at sill and control marsh sites. This result may be a consequence of high variability in seagrass shoot density and patchiness of seagrass cover at the marsh sill and control sites (Figure 4.3D). Additionally, the unvegetated corridor between the sill or control marsh and the beginning of a seagrass patch was typically 5 m or greater in length, which could have precluded nekton from crossing readily to utilize both structured habitats cite a Minello paper here. Sandflat or mudflat corridors between structured habitats may have higher predation rates than vegetated habitats and may serve as a barrier between habitats for juvenile nekton (Irlandi and Crawford 1997, Micheli and Peterson 1999, Jelbart et al. 2006, Rozas et al. 2011).

Comparison of sills to control marshes and bulkheads

Higher abundances of fishes at sill sites relative to bulkhead sites indicated that the unvegetated habitat adjacent to sills was serving as a more suitable habitat for fishes than the unvegetated habitat adjacent to bulkheads (Figure 4.6A-B). The difference in catch rates was driven primarily by the absence of resident fishes such as *F. heteroclitus* and *F. majalis* at bulkhead sites (Table 4.2). Although there were no differences in crustacean catch rates between bulkheads and marsh sills, *Palaemonetes* spp., another marsh resident, was also absent from the bulkheaded sites (Table 4.2). Both resident and juvenile transient species benefit from unvegetated edge adjacent to salt marsh (Lipcius et al. 2005); however, resident species also utilize the interior marsh during high tide (Peterson and Turner 1994). This dependency on the marsh interior may explain the absence of resident species at bulkheaded sites.

Bivalves, such as *C. virginica* and mytilid mussels, were the dominant epibiota on sills, while barnacles formed a larger proportion of the cover on bulkheads (Figure 4.6C). Thus, the epibiotic community on sills resembles that of an intertidal oyster reef more so than that on

bulkheads (Wells 1961, Fodrie et al. 2014). Nekton that use intertidal oyster reefs for refuge and food resources, such as oyster toadfish (*Opsanus tau*) and *A. probatocephalus* (Peterson et al. 2003), would likely receive similar benefits from stone sills once the epibiotic community has become established. Additionally, the relief and geometry of a sill is closer to that of an oyster reef than is a vertical bulkhead's geometry. Therefore, a sill is likely to provide refuge and resources more similar to those provided by oyster reefs (Chapman and Blockley 2009, Scyphers et al. 2011). Grabowski et al. (2005) and Geraldi et al. (2009) found that restored oyster reefs adjacent to salt marshes did not enhance abundances and were functionally redundant as fish habitat. However, the reefs constructed in both of those studies were lower in vertical relief and overall footprint than the sills sampled in our study. The marsh vegetation in the Grabowski et al. and Geraldi et al. studies may have also been older and better established than the young, recently planted marshes in our study. Therefore, increases in habitat structural complexity in the previously studied restored oyster reefs may have been less than increases associated with stone sills in our study.

Design, site suitability, monitoring, and adaptive management of living shorelines

To ensure that our results guide improved coastal defense strategies, we identify several aspects of living shorelines that warrant further research. If one major goal of a living shoreline is to sustain or enhance multiple ecosystem services, then additional studies targeting the delivery of all those services are needed. A better understanding of the relationship between sill placement relative to marsh plantings and/or design (e.g., size, distance from shore, number of drop-downs or gaps, orientation relative to shore) and accessibility of intertidal habitat to nekton is needed. For example, historically, the natural orientation of intertidal oyster reefs was often perpendicular to shore; therefore constructing structures to mimic this orientation may better

reflect natural stabilization processes acting on shorelines and may provide greater access of habitat to nekton (Grave 1901). Habitats will likely be more accessible to nekton where channel flows are high and sediment deposition is low landward of a structure (including access for larger, predatory fish: Figure 7), although this model has yet to be tested. Factors such as tidal regime, shoreline geomorphology, local sediment supply, fetch, and storm frequency will influence the trajectory of ecosystem development of a living shoreline and should be considered further (Ruggiero and McDougal 2001, Cahoon 2006, Ranasinghe and Turner 2006). Finally, the type of shallow subtidal habitats (e.g., seagrass or mudflat) that would be replaced by a structure should also be identified and the costs and benefits of habitat trade-offs should be assessed (vis-à-vis ecosystem services: Peterson and Lipcius 2003).

Despite the need for additional research on living shorelines, our results allow us to make some specific recommendations for implementing ecologically sustainable coastal defense strategies. First, we suggest wherever feasible, living shorelines (i.e. vegetation alone or, if necessary due to higher rates of erosion, vegetation with a sill) be used to stabilize a shoreline in lieu of bulkheads to provide better habitat for nekton. Also, sites should be monitored for a minimum of three years after construction and periodically thereafter to ensure that vegetation has become established, epibiota have colonized structures, and nektonic organisms are able to access the marsh using the methodology presented in this paper. If vegetation has not become established after three years, additional planting may be required. If nekton access is compromised, additional openings or a reduction in the height of the structure may be necessary to increase water flow or decrease sedimentation. Careful design and management of living shorelines may sustain ecosystem services, such as habitat provision and erosion protection, even as sea levels rise (Rodriguez et al. 2014) and storminess increases (Arkema et al. 2013).

Therefore, living shorelines should be considered further as a preferred option for shoreline protection that simultaneously enhances the ecosystem service of habitat enhancement for fish and mobile crustaceans.

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TABLES

Table 4.1. Catch rates (individuals per 6 hrs, high to low tide and g per 6 hrs) and mean standard length (mm) of species caught in salt marsh habitat at CI sill and control marsh sites.

			Sill		Control				
Speciesª	BACI [♭]	Ind. 6hr-1	g 6hr-1	SL (mm)	Ind. 6hr-1	g 6hr-1	SL (mm)		
Fish									
Mugil species (T)	Р	109.1(65.9)	966.8(490.6)	91.2(1.8)	9.6(6.0)	190.3(124.5)	89.8(4.0)		
Lagodon rhomboides (T)	Р	104.5(7.9)	543.0(134.9)	54.1(0.8)	63.8(16.5)	457.9(134.9)	58.4(1.0)		
Leiostomus xanthurus (T)	Р	18.4(5.5)	72.1(9.8)	56.4(1.1)	5.7(2.5)	19.9(9.9)	51.5(1.1)		
Eucinostomus species (T)	Р	9.7(3.7)	23.9(9.1)	43.0(1.2)	1.1(0.1)	1.9(0.2)	46.0(4.4)		
Fundulus heteroclitus (R)		9.6(4.1)	41.5(20.4)	48.5(0.8)	1.3(1.0)	3.2(1.8)	45.9(1.9)		
Fundulus majalis (R)		5.5(1.8)	27.2(10.5)	58.7(2.1)	0.4(0.1)	1.9(0.8)	61.4(4.9)		
<i>Menidia menidia</i> (R)		2.0(2.0)	2.0(1.5)	45.5(2.8)	0.1(0.1)	0.1(0.0)	41.0(0.0)		
Paralichthys species (T)	Р	1.9(0.7)	87.6(8.7)	141.7(17.3)	0.5(0.2)	58.7(36.2)	223.6(50.0)		
Cynoscion nebulosus (T)	Р	1.4(0.5)	10.9(2.8)	63.7(7.6)	0.4(0.1)	19.4(10.0)	117.6(27.9)		
Orthopristis chrysoptera (T)		1.4(0.5)	21.2(6.9)	80.7(3.8)	0.7(0.3)	14.7(6.1)	89.5(6.1)		
Bairdiella chrysoura (T)		1.0(0.1)	24.1(5.5)	106.3(5.2)	0.6(0.2)	14.4(2.7)	102.0(10.9)		
Menidia beryllina (R)	Р	0.5(0.3)	1.0(0.7)	55.9(3.5)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Cyprinodon variegatus (R)		0.4(0.4)	1.4(1.4)	42.3(1.6)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Symphurus plagiusa (T)	Р	0.4(0.1)	1.3(0.6)	59.5(7.4)	0.1(0.1)	0.1(0.1)	41.3(4.3)		
Anchoa mitchilli (T)	Р	0.4(0.3)	0.2(0.3)	48.7(2.4)	0.1(0.1)	0.4(0.2)	69.0(0.0)		
Lutjanus griseus (T)		0.4(0.2)	0.5(0.3)	33.8(5.0)	0.1(0.1)	0.1(0.1)	36.0(1.0)		
Sciaenops ocellatus (T)	Р	0.2(0.1)	20.6(10.5)	181.7(17.0)	0.1(0.1)	15.8(15.8)	245.5(94.5)		
Strongylura marina (T)		0.2(0.0)	0.8(0.3)	148.3(24.9)	0.4(0.3)	1.4(1.4)	64.6(32.3)		
Anguilla rostrata (T)		0.1(0.1)	11.8(7.8)	413.0(107.0)	0.1(0.1)	20.7(20.7)	468.5(46.5)		
Opsanus tau (R)	Р	0.1(0.1)	48.6(48.6)	207.0(37.0)	0.1(0.1)	16.2(16.2)	204.0(0.0)		
Archosargus probatocephalus (T	Γ)	0.1(0.1)	0.1(0.0)	25.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Chasmodes saburrae (T)		0.1(0.1)	0.1(0.1)	50.0(0.0)	0.1(0.1)	0.3(0.3)	53.0(0.0)		
Hypsoblennius hentz (T)		0.1(0.1)	0.1(0.1)	45.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Sphyraena barracuda (T)		0.1(0.1)	12.5(12.5)	190.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Sphyraena borealis (T)		0.1(0.1)	1.0(1.0)	127.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)		
Trachinotus falcatus (T)		0.1(0.1)	0.1(0.1)	35.0(0.0)	0.1(0.1)	0.0(0.0)	0.0(0.0)		
Oligoplites saurus (T)		0.0(0.0)	0.0(0.0)	0.0(0.0)	0.1(0.1)	0.1(0.1)	35.0(0.0)		
Synodus foetens (T)		0.0(0.0)	0.0(0.0)	0.0(0.0)	0.1(0.1)	0.3(0.3)	83.0(0.0)		
Crustaceans									
Palaemonetes species (R)	Р	31.9(15.0)	7.1(3.4)	22.0(0.3)	2.3(1.7)	0.4(0.3)	21.6(0.5)		
Callinectes sapidus (T)	Р	18.0(5.6)	728.6(70.1)	74.3(1.9)	12.0(2.1)	554.9(120.6)	74.6(2.3)		
Penaeus species (T)	Р	9.4(1.0)	17.4(5.0)	49.3(1.4)	1.9(0.5)	5.5(1.5)	55.9(3.2)		
Menippe mercenaria (T)		0.1(0.1)	14.3(14.3)	196.0(0.0)	0.1(0.1)	17.1(17.1)	79.0(0.0)		

^aTransient species are defined as fishes that spend only a portion of their life cycle in the estuary and are denoted with a (T). Resident species spend their entire life cycle within the estuary and are denoted with a (R) - after Peterson and Turner 1994 and Hettler 1989.

^bSpecies that were caught within the marsh at the BACI PKS sill site post-construction are denoted with a "P".

Table 4.2. Catch rates (individuals per 4 hrs, 2 hours before and 2 hours after high tide, and g per 4 hrs) and mean standard length (mm) of species caught in salt marsh edge habitat at sill, control marsh and bulkhead sites.

			S	Sill					Co	ntrol					Bul	khead		
	Ind.		S	SL Ind. 4hr-					Ind.									
Species ^ª	4h	r-1	g 4	hr-1	(m	ım)		1	g 4	hr-1	SL (mm)	4hr-1		g 4hr-1		SL (mm)	
Fish																		
Fundulus	23	(9.	79	(30	51	(0.	1.	(0.6	8.	(4.	60.	(29	0.	(0.	0.	(0.		(0.
heteroclitus (R)	.7	0)	.3	.3)	.1	6)	3)	2	1)	2	.8)	0	0)	0	0)	0.0	0)
Lagodon	4.	(2.	20	(7.	50	(1.	10	(2.7	44	(15	54.	(1.	5.	(2.	21	(12	53.	(0.
rhomboides (T)	7	7)	.4	5)	.8	1)	.2)	.1	.3)	3	6)	2	4)	.7	.2)	8	9)
Fundulus majalis	0.	(0.	3.	(2.	57	(5.	0.	(0.2	1.	(1.	70.	(15	0.	(0.	0.	(0.		(0.
(R)	9	2)	8	5)	.9	3)	2)	2	2)	0	.8)	0	0)	0	0)	0.0	0)
Orthopristis	0.	(Ó.	4.	(1.	63	(Ź.	1.	(0.2	9.	(Ź.	62.	21.	0.	(Ó.	4.	(Ź.	67.	(Ś.
chrysoptera (T)	7	2)	7	9)	.3	à)	7)	2	8)	4	9)	5	2)	1	2)	3	Ž)
Cyprinodon	0.	(Ó.	1.	(Ó.	38	(Í.	0.	(0.0	0.	(Ó.		(Ó.	0.	(Ó.	0.	(Ó.		(Ó.
variegatus (R)	5	3)	0	5)	.3	7)	0)	0	Ò)	0.0	Ò)	0	Ò)	0	Ò)	0.0	Ò)
Archosarqus	0.	(Ó.	0.	(Ó.	40	(Í.	0.	(0.0	0.	(Ó.		(Ó.	0.	(Ó.	0.	(Ó.		(Ó.
probatocephalus (T)	3	3)	8	8)	.8	5)	0)	0	ò)	0.0	ò)	0	ò)	0	ò)	0.0	Ò)
, Eucinostomus	0.	(Ó.	0.	(Ó.	39	(Ó.	0.	(0.0	0.	(Ó.		(Ó.	0.	(Ó.	0.	(Ó.		(Ó.
species (T)	1	1)	2	3)	.0	Ò)	0)	0	ò)	0.0	ò)	0	ò)	0	Ò)	0.0	Ò)
Cvnoscion	0.	(Ó.	0.	(Ó.	95	(Ó.	0.	(0.0	0.	(Ó.		(Ó.	0.	(Ó.	0.	(Ó.		(Ó.
nebulosus (T)	1	1)	8	8)	.0	Ò)	0)	0	Ò)	0.0	Ò)	0	0)	0	Ò)	0.0	Ò)
	0.	(Ó.	0.	(0.	51	(0.	0.	, (0.1	1.	(1.	80.	(0.	0.	(0.	0.	(Ó.	71.	(Ó.
Lutjanus griseus (T)	1	1)	2	2)	.0	0)	1)	0	() 0)	0	0)	1	1)	7	6)	0	0)
Symphurus plagiusa	0.	(0.	0.	(Ó.	0.	(0.	0.	, (0.1	0.	(0.	15	(0.	0.	(0.	0.	(0.	Ū	(0.
(T)	0	0)	0	0)	0	0)	1)	1	1)	1.0	0)	0	0)	0	0)	0.0	0)
(.)	0.	(0.	0.	(0.	0.	(0.	0.	, (0.0	0.	(Ó.		(0.	0.	(0.	3.	(3.	31	(0.
Anguilla rostrata (T)	0	0)	0	0)	0	0)	0)	0	0)	0.0	0)	1	1)	0	1)	0.0	0)
Hvpsoblennius hentz	0.	(0.	0.	(0.	0.	(0.	0.	, (0.1	0.	(0.	44.	(0.	0.	(0.	0.	(0.	0.0	(0.
(T)	0	0)	0	0)	0	0)	1)	2	1)	5	0)	0	0)	0	0)	0.0	0)
Crustaceans																		
Palaemonetes	1.	(0.	0.	(0.	23	(0.	0.	(0.0	0.	(0.	23.	(0.	0.	(0.	0.	(0.		(0
species (R)	5	7)	3	2)	.4	7)	3	.7)	1	0)	5	0)	0	0)	0	0)	0.0	0)
	0.	(0.	0.	(0.	67	(4.	0.	(0.1	0.	(0.	52.	(3.	0.	(0.	1.	(1.	69.	(5
Penaeus species (T)	1	Ì)	5	3)	.0	Ò)	5)	8	7)	8	1)	2	2)	0	Ì)	7	Ž)
Panopeus herbstii	0.	(Ó.	0.	(Ó.	29	(Ó.	0.	(0.0	0.	(Ó.		(Ó.	0.	(Ó.	0.	(Ó.		(Ó
(R)	1	1)	5	5)	.0	ò)	0)	0	ò)	0.0	ò)	0	ò	0	ò)	0.0	ò)

^aTransient species are defined as fishes that spend only a portion of their life cycle in the estuary and are denoted with a (T). Resident species spend their entire life cycle within the estuary and are denoted with a (R) - after Peterson and Turner 1994 and Hettler 1989

FIGURES

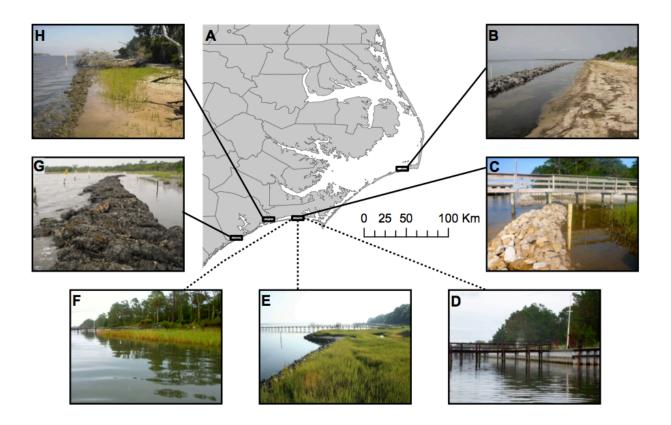


Figure 4.1. a) Map of locations of (b) the BACI sill and control marsh site on Hatteras Island, Outer Banks, NC; (c) the BACI sill, (d) the bulkhead, (e) the CI sill, and (f) control marsh sites in Pine Knoll Shores (PKS), NC; (g) the BACI oyster bag sill and control marsh site at Morris Landing, Holly Ridge, NC; and (h) the BACI oyster bag sill and control marsh site on Jones Island, Swansboro, NC. The BACI control marsh sites are not pictured. Solid lines to photographs indicate BACI sites and dotted lines to photographs indicate CI sites.

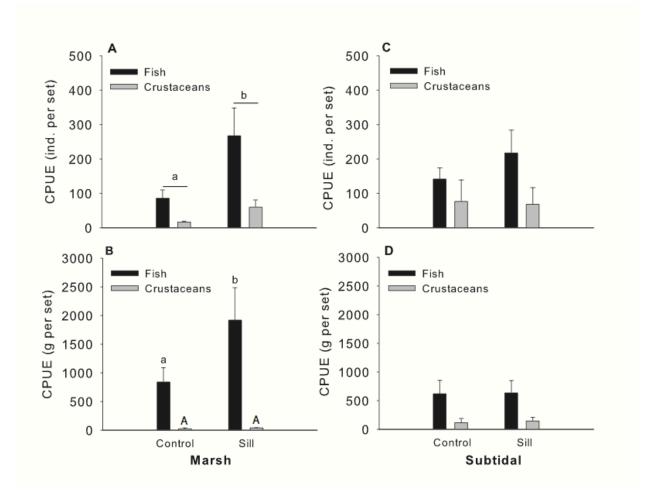


Figure 4.2. Mean a) CPUE, individuals per fyke net set, in salt marsh; b) CPUE, grams per fyke net set, in salt marsh; c) CPUE, individuals per seine net set, in subtidal habitats; and d) CPUE, grams per seine net set, in subtidal habitats. Error bars are \pm standard error (SE). Black bars with different lower case letters ("a" or "b") and gray bars with different upper case letters ("A" or "B") are significantly different (*P*<0.05).

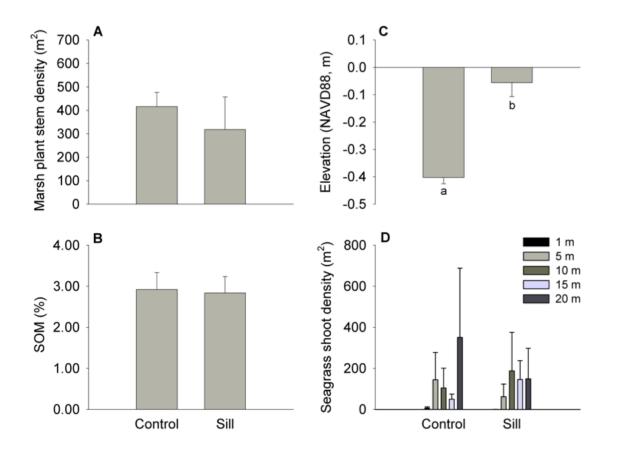


Figure 4.3. Mean a) total stem density across all species of marsh macrophytes; b) SOM (%); surface elevation (NAVD88, m) of the mudflat within one meter seaward of marsh edge; and d) total seagrass shoot density across all species with increasing distance from the marsh edge (1 m to 20 m) at CI control and sill sites. Error bars are \pm standard error (SE). Bars with different lower case letters ("a" or "b") are significantly different (*P*<0.05).

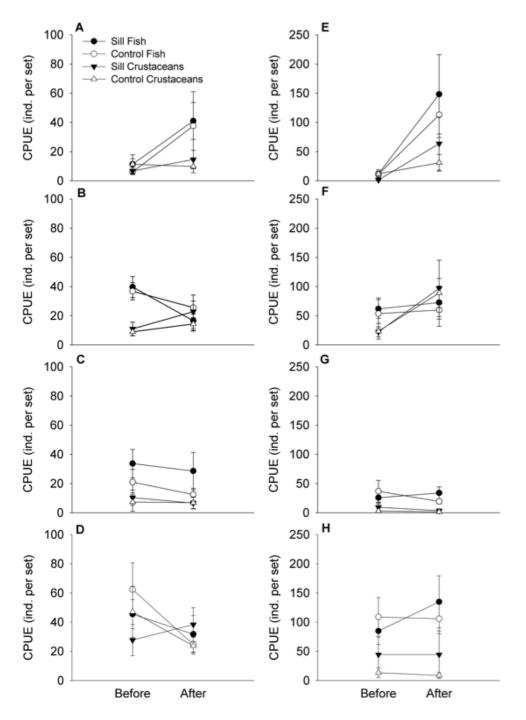


Figure 4.4. Mean CPUE (individuals per set) before and after construction of the sill at Hatteras, Pine Knoll Shores, Jones Island, and Morris Landing in salt marsh (fyke net, a-d, respectively) and subtidal habitat (seine net, e-h, respectively). Error bars are \pm standard error (SE).

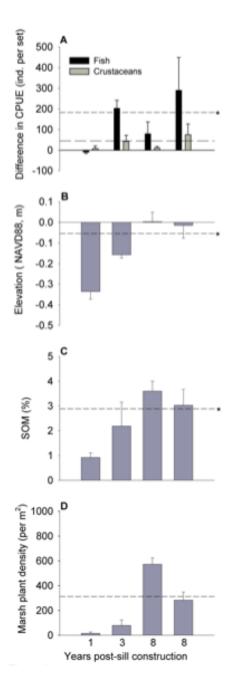


Figure 4.5. a) Change in fish CPUE (individuals per fyke net set) and crustacean CPUE between BACI (<1-y post-construction) and CI (3-yrs [one site] and 8-yrs [two sites] post-construction) sill and control marsh sites in PKS. The short dashed line represents the mean change in fish CPUE of the 3 CI sill sites and the long dashed line represents the mean change in crustacean CPUE of the 3 CI sill sites. b) Mean surface elevation (NAVD88, m) of the mudflat within one meter landward of the sill; c) Mean SOM (%); and d) Mean density (per m²) of marsh macrophytes at BACI and CI sill sites. The short dashed line represents the mean surface elevation, SOM, or stem density of marsh macrophytes of the 3 CI sill sites. An "*" indicates that this mean is significantly different from the mean of the BACI sill site one year after sill construction (P<0.05). Error bars are ± standard error (SE).

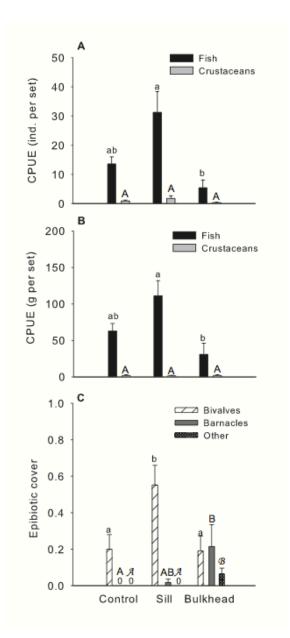
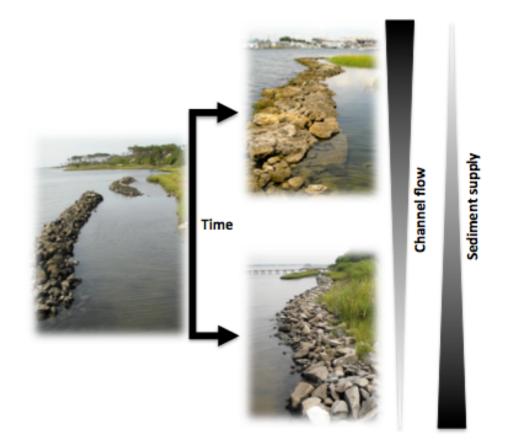
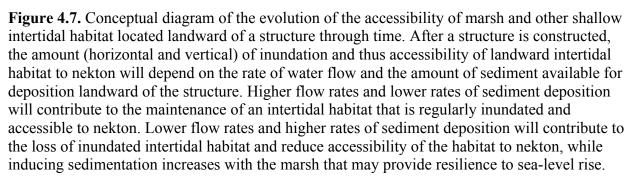


Figure 4.6. Mean fish and crustacean CPUE: a) individuals per trap set and b) grams per trap set along the unvegetated edge of sills, control marshes, and bulkheads. c) Proportion of coverage of bivalves (oysters and ribbed mussels), barnacles, other epibiota (tunicates, bryozoans, and sponges) on stone sills, on the sand/mud substrate the edge of control marshes, and on bulkheads. Black bars or striped bars with different lower case letters ("a" or "b"), light gray bars or dark gray bars with different upper case letters ("A" or "B"), and black dotted bars with different upper case cursive letters ("A" or "B") are significantly different (P<0.05). Error bars are ± SE.





APPENDIX 1.A: VERIFICATION OF SUCCESSFUL PERIWINKLE AND FIDDLER CRAB DENSITY MANIPULATIONS

Methods

To ensure that shading did not influence our results, we took photosynthetically active radiation (PAR) measurements in the afternoon (when the sun is at an angle that would result in shading) inside at 30 cm above the base of the enclosure (mean height of the S. alterniflora plants), inside at the base of the enclosure, and outside of our enclosures. After removing all fiddler crabs and periwinkles from the enclosed plots, we added marsh periwinkles with shell height of at least 18 mm and female U. pugnax and U. pugilator with a carapace width of 10 mm or greater back to the addition treatment plots. Female crabs were used because their feeding rates and burrow occupation time is higher than males (Weissburg 1993, Hemmi 2003). We recorded wet weights (g), measured (shell length or carapace width, mm), and numbered each periwinkle and fiddler crab (using a sharpie marker and superglue as a sealant) prior to adding them to the plots. Bi-weekly in June, July, and August, we handpicked fiddler crabs and marsh periwinkles from the removal plots. At the conclusion of the experiment, we recovered labeled periwinkles from periwinkle addition treatment plots and recorded fiddler crab burrows in fiddler addition treatment plots. Individual fiddler crabs added to the enclosures were not recovered at the conclusion of the experiment.

Results

There was no significant difference in the light measurements (PAR) taken inside of the enclosure at 30 cm above the base (mean height of *S. alterniflora* plants in the enclosures, $3142\pm75 \ \mu mol \ s^{-1} \ m^{-2}$) and outside of the enclosures ($3425\pm65 \ \mu mol \ s^{-1} \ m^{-2}$, $P > 0.05 \ Tukey's$

posthoc test). PAR was lower at the base of the enclosure (2647 \pm 8 µmol s⁻¹ m⁻²) when compared to the PAR outside and the PAR at 30 cm above the base of the enclosure (P < 0.05, Tukey's posthoc test). PAR taken at the base of the enclosure are assumed to be equivalent to light measurements to within a stand of S. alterniflora, which would be self-shading at this height, therefore we assume that the enclosures did not result in additional shading of our treatment plots. Ambient densities of marsh periwinkles and fiddler crabs did not differ between treatments prior to density manipulations (Table 1.A1). At the conclusion of the experiment, there was no difference in the number of marsh periwinkles between the periwinkle addition treatments (with and without fiddler crabs) or in the number of fiddler crab burrows between the fiddler crab addition treatments (with and without periwinkles) (Tables 1.A1, 1.A3). We recovered 215±8 of the 300 periwinkles after Hurricane Irene, indicating that although some periwinkles were lost during the experiment, a majority of the periwinkles remained in the plots post-Hurricane (Figure 1.A1). Mean shell growth, change in wet weight (g), and dry tissue to shell proportion of marsh periwinkles did not differ between periwinkle addition treatments (Tables 1.A2, 1.A4). A majority of the marsh periwinkles removed after initial periwinkle removal were less than 18mm in shell length and a majority of the crabs removed after the initial crab removal were males or juveniles (less than one cm carapace length). We did not observe any effects of marsh periwinkles on abundance of fiddler crabs in the plots, based on the densities of burrows remaining at the conclusion of the experiment.

Table 1.A1. The number of periwinkles and fiddler crabs present in the plots prior to experimental manipulations, removed from the removal treatments during the experiment, and counted within the addition plots at the conclusion of the experiment. Error bars present \pm 1 SE (n= 6).

Treatments	Pre- treatment fiddler crab density	Pre- treatment periwinkle density	Fiddler crabs removed	Periwinkles removed	Final periwinkle count	Final fiddler crab burrow count
Open (ambient densities)	29 ± 16	18 ± 3	NA	NA	NA	NA
Periwinkle addition & fiddler crab removal	21 ± 3	29 ± 7	95 ± 7	NA	211 ± 14	NA
Periwinkle & fiddler crab addition	26 ± 3	25 ± 4	NA	NA	213 ± 7	65 ± 7
Periwinkle removal & fiddler crab addition	22 ± 4	39 ± 16	NA	174 ± 30	NA	55 ± 7
Periwinkle & fiddler crab removal	23 ± 3	27 ± 6	92 ± 9	173 ± 36	NA	NA

Table 1.A2. The shell growth (mm), change in wet weight (g), and final body mass proportion
(g tissue/g shell dry weight) of labeled periwinkles recovered at the conclusion of the
experiment. Error bars present ± 1 SE (n= 6).

Treatments	Shell growth (mm)	Change in wet weight (g)	Body mass proportion (g tissue/g shell dry weight)
Open (ambient densities)	NA	NA	NA
Periwinkle addition & fiddler crab removal	0.15 ± 0.16	0.07 ± 0.19	0.06 ± 0.02
Periwinkle & fiddler crab addition	0.18 ± 0.18	0.45 ± 0.24	0.06 ± 0.02
Periwinkle removal & fiddler crab addition	NA	NA	NA
Periwinkle & fiddler crab removal	NA	NA	NA

Table 1.A3. ANOVA results for periwinkle and fiddler crab initial (pre-treatment) densities, removals, and final counts at the conclusion of the experiment. P < 0.05 are in bold.

Response Variable						
Pre-treatment fiddler crab			Sum of	Mean		
density	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	4	263.2	65.8	0.9371	0.4587
	Error	25	1755.5	70.22		
Pre-treatment periwinkle			Sum of	Mean		
density	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	4	1458.53	364.63	0.804	0.5342
	Error	25	11338.67	453.55		
Fiddler crabs removed	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
	Туре	1	24.0833	24.083	0.06	0.8114
	Error	10	4010.8333	401.083		
Periwinkles removed			Sum of	Mean		
	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	1	3	3	0.0005	0.9834
	Error	10	66275	6627.5		
Final periwinkle count			Sum of	Mean		
	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	1	14.0833	14.083	0.02	0.8903
	Error	10	7034.8333	703.483		
Final fiddler crab burrow count	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
	Туре	1	320.3333	320.333	1.1797	0.3029
	Error	10	2715.3333	271.533	-	

Table 1.A4. ANOVA results for periwinkle shell growth (mm), change in wet weight (g), and final body mass proportion (g tissue/g shell dry weight). P < 0.05 are in bold.

Response Variable			AN	OVA Results		
Shell growth (mm)	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
	Туре	1	0.0007	0.0007	0.0224	0.8841
	Error	10	0.3224	0.03224		
Change in wet weight (g)			Sum of	Mean		
	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	1	0.0008	0.0008	0.2994	0.5963
	Error	10	0.0255	0.0025		
Body mass proportion (g tissue/g			Sum of	Mean		
shell dry weight)	Source	DF	Squares	Square	F Ratio	Prob > F
	Туре	1	0	0	0.0285	0.8692
	Error	10	0.0002	0		

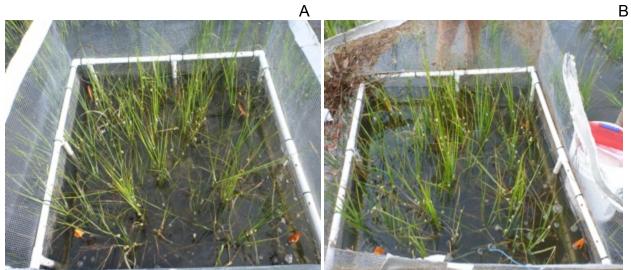


Photo credit: R. Gittman

Photo credit: R. Gittman

Figure 1.A1. Photograph of A) a periwinkle addition and fiddler crab removal enclosure one day before the landfall of Hurricane Irene on a rising tide; and B) the same periwinkle addition and fiddler crab removal enclosure two days post-Hurricane Irene on a rising tide.

APPENDIX 1.B: ANALYSIS OF CARBON AND NITROGEN CONTENT IN S. ALTERNIFLORA SHOOTS FROM TREATMENTS

Table 1.B1. Carbon (content by dry weight, %), Nitrogen (content by dry weight, %), and Carbon to Nitrogen ratio (C:N) of youngest shoot of *S. alterniflora* stems (n=10) per treatment plot (n=6). Values represent means \pm SE.

Treatment	Carbo	on (%) ^b	Nitro	gen	(%) ^b	С	:N ^b	
Open (ambient densities) ^a	42.89	±	0.19	1.81	±	0.07	27.85	±	1.09
Fiddler crab & periwinkle removal	42.62	±	0.23	1.71	±	0.09	29.39	±	1.50
Fiddler crab addition & periwinkle removal	42.65	±	0.43	1.78	±	0.08	28.18	±	1.27
Fiddler crab & periwinkle addition	42.75	±	0.28	1.80	±	0.06	27.87	±	1.02
Periwinkle addition & fiddler crab removal	42.39	±	0.43	1.89	±	0.10	26.55	±	1.38

^a The open treatment contains ambient, unmanipulated densities of marsh periwinkles and fiddler crabs and does not have an enclosure.

^b There were no differences in C, N, and C:N across treatments (p>0.05, *see* Tables 1.B2-4).

Table 1.B2. ANOVA and *a priori* planned comparisons results comparing the Carbon content (%) of *S. alterniflora* leaf tissue between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle & fiddler crab removal treatment is compared to all other treatments except open treatment; Comparison 3: fiddler crab addition treatments (regardless of periwinkle treatment) are compared to periwinkle addition & fiddler crab removal treatment is compared to periwinkle treatment; and Comparison 4: periwinkle addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition treatment. *P* < 0.05 are in bold.

One-way		Sum of			
ANOVA	DF	squares	Mean square	F ratio	Prob > F
Model	4	0.81	0.20	0.3111	0.8678
Error	25	16.20	0.65		
Planned comparis	sons				
Treatments		Comparison 1 ^a	Comparison 2	Comparison 3	Comparison 4
Open (ambient der Periwinkle addition	,	+	NA	NA	NA
removal		-	+	+	+
Periwinkle & fiddlen Periwinkle removal addition		-	+	-	- NA
Periwinkle & fiddle	r crab removal	-	-	NA	NA
Partitioned Sum of	of Squares	0.3922	0.0020	0.3803	0.0320
t Ratio		0.7779	-0.0556	0.7660	-0.2223
Prob> t		0.4439	0.9561	0.4508	0.8259

Table 1.B3. ANOVA and planned comparisons results comparing the Nitrogen content (%) of *S. alterniflora* leaf tissue between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle & fiddler crab removal treatment is compared to all other treatments except open treatment; Comparison 3: fiddler crab addition treatments (regardless of periwinkle treatment) are compared to periwinkle addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition treatment. *P* < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F
Model	odel 4		0.02	0.611	0.6587
Error	25	0.95	0.04		
Planned compar	isons				
Treatments		Comparison 1 ^a	Comparison 2	Comparison 3	Comparison 4
Open (ambient de Periwinkle additio removal	,	+	NA +	NA +	NA +
Periwinkle & fiddle Periwinkle remova		-	+	-	-
addition		-	+	-	NA
Periwinkle & fiddle	er crab removal	-	-	NA	NA
Partitioned Sum	of Squares	0.0008	0.0539	0.0367	0.0010
t Ratio		0.1455	1.1935	-0.9853	-0.1632
Prob> t		0.8855	0.2439	0.3339	0.8716

Table 1.B4. ANOVA and planned comparisons results comparing the C:N ratio of *S. alterniflora* leaf tissue between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle & fiddler crab removal treatment is compared to all other treatments except open treatment; Comparison 3: fiddler crab addition treatments (regardless of periwinkle treatment) are compared to periwinkle addition & fiddler crab removal treatment is compared to periwinkle addition & fiddler crab removal treatment is compared to periwinkle addition & fiddler crab removal treatment is compared to periwinkle & fiddler crab addition treatment is compared to periwinkle & fiddler crab addition treatment is compared to periwinkle & fiddler crab addition treatment is compared to periwinkle & fiddler crab addition treatment is compared to periwinkle & fiddler crab addition treatment. *P* < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F
Source	4	24.60	6.15	0.642	0.6375
Model	25	239.50	9.58		
Planned compar	risons	Comparison 1			
Treatments		а	Comparison 2	Comparison 3	Comparison 4
Open (ambient de Periwinkle additio	,	+	NA	NA	NA
removal		-	+	+	+
Periwinkle & fiddl Periwinkle remov		-	+	-	-
addition		-	+	-	NA
Periwinkle & fiddl	er crab removal	-	-	NA	NA
Partitioned Sum	of Squares	0.1072	15.57	8.64	0.2813
t Ratio		-0.1058	-1.2751	0.9497	0.1714
Prob> t		0.9166	0.2140	0.3514	0.8653

APPENDIX 1.C: ANOVA AND PLANNED COMPARISONS RESULTS FOR S. ALTERNIFLORA CHANGE IN STEM DENSITY, ABOVE-GROUND BIOMASS, PROPORTION OF SCARRED TO TOTAL LEAF LENGTH, CHANGE IN SUMMED LIVE STEM HEIGHTS, AND BELOW-GROUND BIOMASS.

Table 1.C1. ANOVA and *a priori* planned comparisons results comparing the change in *S. alterniflora* stem density from the beginning to the end of the experiment between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle addition treatments are compared to periwinkle removal treatments (regardless of fiddler crab treatment); Comparison 3: periwinkle & fiddler crab addition treatment is compared to periwinkle addition 4: periwinkle removal & fiddler crab addition treatment is compared to periwinkle & fiddler crab removal treatment; and Comparison 4: periwinkle removal & fiddler crab addition treatment is compared to periwinkle & fiddler crab removal treatment. *P* < 0.05 are in bold.

		Sum of			
One-way ANOVA	DF	squares	Mean square	F ratio	Prob > F
Model	4	83.80	20.95 0.9778		0.4374
Error	25	535.67	21.43		
Planned comparisons					
Treatments		Comparison 1 ^a	Comparison 2	Comparison 3	Comparison 4
Open (ambient densitie	s)	+	NA	NA	NA
Periwinkle addition & fic	dler				
crab removal Periwinkle & fiddler cral	n	-	+	+	NA
addition	0	-	+	-	NA
Periwinkle removal & fig	ddler				
crab addition Periwinkle & fiddler cral	•	-	-	NA	+
removal	0	-	-	NA	-
Partitioned Sum of Sq	uares	7.01	18.38	56.33	2.083
t Ratio		-0.5719	-0.9261	-1.6215	-0.312
Prob> t		0.5725	0.3633	0.1175	0.7578

Table 1.C2. ANOVA and *a priori* planned comparisons results comparing the total aboveground biomass (g dry weight) of *S. alterniflora* at the conclusion of the experiment between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle addition treatments are compared to periwinkle removal treatments (regardless of fiddler crab treatment); Comparison 3: periwinkle & fiddler crab addition treatment is compared to periwinkle addition & fiddler crab removal treatment; and Comparison 4: periwinkle removal & fiddler crab addition treatment is compared to periwinkle & fiddler crab removal treatment. P < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F	
Model	Model 4		62.95	1.310	0.2933	
Error	25	1201.12	48.04			
Planned comparisons	5					
Treatments		Comparison 1 ^a	Comparison 2	Comparison 3	Comparison 4	
Open (ambient densitie Periwinkle addition & fi	,	+	NA	NA	NA	
removal		-	+	+	NA	
Periwinkle & fiddler cra Periwinkle removal & fi		-	+	-	NA	
addition		-	-	NA	+	
Periwinkle & fiddler cra	b removal	-	-	NA	-	
Partitioned Sum of So	quares	1.89	217.67	21.57	10.68	
t Ratio		-0.1986	2.128	0.6700	-0.471	
Prob> t		0.8442	0.0433	0.5090	0.6414	

Table 1.C3. ANOVA and *a priori* planned comparisons results comparing the proportion of total scarred leaf length to total leaf length of *S. alterniflora* at the conclusion of the experiment between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle addition treatments are compared to periwinkle removal treatments (regardless of fiddler crab treatment); and Comparison 3: periwinkle & fiddler crab addition treatment is compared to periwinkle addition treatment between treatment. *P* < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F
Model	4	0.2400	0.0600	33.98	<0.0001
Error	25	0.0441	0.0018		
Planned comparisons	5		Comparison	Comparison	Comparison
Treatments			1 ^a	2	3
Open (ambient densitie	es)		+	NA	NA
Periwinkle addition & fig	ddler crab r	emoval	-	+	+
Periwinkle & fiddler cra	b addition		-	+	-
Periwinkle removal & fi	ddler crab a	addition	-	-	NA
Periwinkle & fiddler cra	b removal		-	-	NA
Partitioned Sum of Sc	quares		0.0335	0.2064	0.0000
t Ratio			-4.35	-10.81	0.1400
Prob> t			0.0002	<0.0001	0.8913

Table 1.C4. ANOVA and *a priori* planned comparisons results comparing the change in the summed live stem heights (cm) of *S. alterniflora* between the beginning and the end of the experiment between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; Comparison 2: periwinkle addition treatments are compared to periwinkle removal treatments (regardless of fiddler crab treatment); Comparison 3: periwinkle & fiddler crab addition treatment is compared to periwinkle addition & fiddler crab removal treatment; and Comparison 4: periwinkle removal & fiddler crab addition treatment is compared to periwinkle & fiddler crab removal treatment. P < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F
Model	Model 4		52088	3.26	0.0279
Error	25	399676	15987		
Planned comparisons	i				
Treatments		Comparison 1 ^ª	Comparison 2	Comparison 3	Comparison 4
Open (ambient densitie Periwinkle addition & fig	,	+	NA	NA	NA
removal		-	+	+	NA
Periwinkle & fiddler cral Periwinkle removal & fid		-	+	-	NA
addition		-	-	NA	+
Periwinkle & fiddler cral	b removal	-	-	NA	-
Partitioned Sum of Sq	luares	22.97	77487	124807	6035
t Ratio		-0.04	2.20	2.79	-0.614
Prob> t		0.9701	0.0371	0.0098	0.5445

Table 1.C5. ANOVA and *a priori* planned comparisons results comparing total below-ground biomass of *S. alterniflora* (g dry weight) at the conclusion of the experiment between treatments. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; and Comparison 2: fiddler crab addition treatments are compared to fiddler crab removal treatments (regardless of periwinkle treatment). P < 0.05 are in bold.

One-way ANOVA	DF	Sum of squares	Mean square	F ratio	Prob > F
Model	4	288.09	72.02	1.8243	0.1585
Error	23	908.00	39.48		
Planned comparison	S			Comparison	Comparison
Treatments				1 ^a	2
Open (ambient densiti	ies)			+	NA
Periwinkle addition & f	fiddler crab ı	removal		-	-
Periwinkle & fiddler cra	ab addition			-	+
Periwinkle removal & t	fiddler crab	addition		-	+
Periwinkle & fiddler cra	ab removal			-	-
Partitioned Sum of S	quares			27.21	224.23
t Ratio				-0.8302	-2.3832
Prob> t				0.4150	0.0258

APPENDIX 1.D: STATISTICAL ANALYSIS OF SEDIMENT REDOX POTENTIAL MEASUREMENTS

Table 1.D1. Repeated measures ANOVA results comparing sediment redox potential at a depth of 10 cm at four times during the experiment between treatments. P < 0.05 are in bold.

Repeated Measures ANOVA	Value	Exact F	NumDF	DenDF	Prob>F
F Test	0.5202	3.25	4	25	0.0281
Within Subjects					
Treatment					
Test	Value	Approx_ F	NumDF	DenDF	Prob>F
Wilks' Lambda	0.3475	2.5019	12	61	0.0097
Pillai's Trace	0.8341	2.4069	12	75	0.0108
Hotelling-Lawley	1.3795	2.5554	12	36	0.0147
Roy's Max Root	0.8662	5.4136	4	25	0.0028
Univar unadj Epsilon=	1.0000	2.6727	12	75	0.0048
Univar G-G Epsilon=	0.7433	2.6727	9	56	0.0120
Univar H-F Epsilon=	0.9500	2.6727	11	71	0.0058
Time					
Test	Value	Exact F	NumDF	DenDF	Prob>F
F Test	0.3357	2.5737	3	23	0.0787
Univar unadj Epsilon=	1.0000	2.8990	3	75	0.0405
Univar G-G Epsilon=	0.7433	2.8990	2	56	0.0579
Univar H-F Epsilon=	0.9500	2.8990	3	71	0.0434
Treatment x Time					
Test	Value	Approx_ F	NumDF	DenDF	Prob>F
Wilks' Lambda	0.3475	2.5019	12	61	0.0097
Pillai's Trace	0.8341	2.4069	12	75	0.0108
Hotelling-Lawley	1.3795	2.5554	12	36	0.0147
Roy's Max Root	0.8662	5.4136	4	25	0.0028
Univar unadj Epsilon=	1.0000	2.6727	12	75	0.0048
Univar G-G Epsilon=	0.7433	2.6727	9	56	0.0120
Univar H-F Epsilon=	0.9500	2.6727	11	71	0.0058

Table 1.D2. One-way ANOVA and *a priori* planned comparison results comparing sediment redox potential at a depth of 10 cm on June 14th immediately after enclosure installation but prior to treatment implementation. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; and Comparison 2: fiddler crab addition treatments are compared to fiddler crab removal treatments (regardless of periwinkle treatment). P < 0.05 are in bold.

One-way ANOVA	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	4	65676.27	16419.07	2.73	0.0519
Error	25	150524.21	6020.97		
Planned comparisons					
Treatments				Comparison 1 ^ª	Comparison 2
Open (ambient densities) Periwinkle addition & fiddler crab)			+	NA
removal				-	-
Periwinkle & fiddler crab addition Periwinkle removal & fiddler crab addition				-	+ +
Periwinkle & fiddler crab removal	l			-	-
Partitioned Sum of					
Squares				41839.47	1023.12
t Ratio				2.64	-0.41
Prob> t				0.0142	0.6837

Table 1.D3. One-way ANOVA and *a priori* planned comparison results comparing sediment redox potential at a depth of 10 cm on June 24^{th} . The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; and Comparison 2: fiddler crab addition treatments are compared to fiddler crab removal treatments (regardless of periwinkle treatment). P < 0.05 are in bold.

One-way ANOVA	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	4	116340.53	29085.13	3.54	0.0201
Error	25	205164.83	8206.59		
Planned comparisons					
Treatments				Comparison 1 ^ª	Comparison 2
Open (ambient densities) Periwinkle addition & fiddler crab removal				+	NA
Periwinkle & fiddler crab addition Periwinkle removal & fiddler crab				-	+
addition				-	+
Periwinkle & fiddler crab removal				-	-
Partitioned Sum of					
Squares				21120.53	51522.67
t Ratio				1.60	2.51
Prob> t				0.1212	0.0191

Table 1.D4. One-way ANOVA and *a priori* planned comparison results comparing sediment redox potential at a depth of 10 cm on July 26th. The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; and Comparison 2: fiddler crab addition treatments are compared to fiddler crab removal treatments (regardless of periwinkle treatment). P < 0.05 are in bold.

One-way ANOVA	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	4	12358.33	3089.58	1.12	0.3676
Error	25	68716.33	2748.65		
Planned comparisons					
Treatments				Comparison 1 ^a	Comparison 2
Open (ambient densities) Periwinkle addition & fiddler crab removal				+	NA
Periwinkle & fiddler crab addition Periwinkle removal & fiddler crab				-	+
addition				-	+
Periwinkle & fiddler crab removal				-	-
Partitioned Sum of					
Squares				20.83	240.67
t Ratio				-0.0871	-0.2959
Prob> t				0.9313	0.7697

Table 1.D5. One-way ANOVA and *a priori* planned comparison results comparing sediment redox potential at a depth of 10 cm on August 30^{th} . The ANOVA compares all treatments, while the planned comparisons are as follows: Comparison 1: open (ambient densities) treatment is compared to all other treatments; and Comparison 2: fiddler crab addition treatments are compared to fiddler crab removal treatments (regardless of periwinkle treatment). *P* < 0.05 are in bold.

One-way ANOVA	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	4	8578.67	2144.67	1.68	0.1850
Error	25	31825.50	1273.02		
Planned comparisons					
Treatments				Comparison 1 ^ª	Comparison 2
Open (ambient densities) Periwinkle addition & fiddler crab				+	NA
removal				NA	-
Periwinkle & fiddler crab addition Periwinkle removal & fiddler crab addition				+	-
Periwinkle & fiddler crab removal				NA	-
Partitioned Sum of					
Squares				3360.21	9.38
t Ratio				-1.62	-0.09
Prob> t				0.1168	0.9323

APPENDIX 1.E: STATISTICAL ANALYSIS OF FIELD SURVEY MEASUREMENTS

Response Variable								
<i>S. alterniflora</i> stem density (L) per m ²	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	2	31.25	31.25	0.1271	0.7256		
	Error	18	4424.5	245.806				
<i>S. alterniflora</i> stem density (D) per m ²	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	1	36.45	36.45	4.5405	0.0471		
	Error	18	144.5	8.0278				
<i>S. alterniflora</i> stem height	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	1	4397.9848	4397.98	60.5935	<.0001		
	Error	18	1306.4722	72.58				
Fiddler crab burrows per m ²	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	1	1881.8	1881.8	46.7077	<.0001		
	Error	18	725.2	40.29				
	Welch's Test (Unequal Variances)							
	F Ratio	DF	DF Denied	Prob > F				
	46.7077	1	13.4467097	<.0001				
Marsh periwinkles per m ²	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	1	1008.2	1008.2	1.4405	0.2456		
	Error	18	12597.8	699.88				
Redox potential (mV)	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F		
	Туре	1	383.69	383.69	0.0459	0.8328		
	Error	18	150452.4	8358.47				

Table 1.E1. ANOVA results comparing die-off fronts to healthy, intermediate marsh zones atHoop Pole Creek Cleanwater Reserve. P < 0.05 are in bold.

Response Variable	ANOVA Results										
S. alterniflora	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
stem density (L) per m ²	Туре	1	4032.8	4032.8	2.6487	0.121					
(L) per m	Error	18	27406.4	1522.58							
S. alterniflora	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
stem density (D) per m^2	Туре	1	11139.2	11139.2	22.1016	0.0002					
(D) per m ²	Error	18	9072	504							
S. alterniflora	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
stem height	Туре	1	826.5149	826.515	8.4786	0.0097					
	Error	17	1657.1966	97.482							
Fiddler crab burrows per	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
m ²	Туре	1	33620	33620	6.6691	0.0188					
	Error	18	90740.8	5041.2							
Marsh periwinkles per m ²	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
P	Туре	1	20	20	0.0168	0.8984					
	Error	18	21467.2	1192.62							
Redox potential	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F					
(mV)	Туре	1	12545.04	12545	2.1539	0.1595					
	Error	18	104836.15	5824.2							

Table 1.E2. ANOVA results comparing die-off fronts to healthy, intermediate marsh zones at the Theodore Roosevelt Natural Area. P < 0.05 are in bold.

Appendices References

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APPENDIX 2.A: SUPPLEMENTAL METHODS AND RESULTS

Estimation of shoreline hardening along the U.S. coast

We estimated the amount of hardened shoreline for each coastal county within the continental United States with available shoreline data from the NOAA Office of Response and Restoration (OR&R) webpage (http://response.restoration.noaa.gov/). The shoreline data are a component of a geodatabase for each state or waterbody region that also includes socioeconomic data, topographic lines, and bird and mammal habitat. Combined, these data were used by NOAA OR&R to determine areas of high risk for future oil spills, referred to as an Environmental Sensitivity Index (ESI). Each ESI geodatabase includes an ESI polyline file with the shoreline classified by habitat type and by shoreline type. The ESI shoreline polylines were developed based on aerial surveys to a resolution of 1:50,000, remotely sensed data, and ground truthing (visits to individual shorelines to assess aerial observations) (Table 2.A1, NOAA 2005). Each shore segment within the shoreline polyline file has a length (miles) and a code for the shoreline type (e.g. 3A). The ESI shoreline type field includes up to three codes, which represent the landward to most seaward habitats. For example, a 10A/3A/4 code represents a salt to brackish marsh (10A) inland of a fine-grain beach (3A), which is inland of a coarse-grain beach (4) on the coast. For the purpose of this study, we created a new classification scheme to merge similar habitat codes and indicate which shoreline segments are hardened (riprap, bulkheads, sea walls) (Table 2.A2).

For shoreline segments that were artificially hardened, the new classification code represents the type of shoreline structure present and the habitat where it is built. For example, 6B/3A (riprap inland of fine- to medium-grained beach) is classified as 3.7 or riprap built on a beach shoreline. Priority is given to the shoreline structure regardless of its position in relation

to other shore types. For segments where two different structures are built on the shoreline, the structure is considered 'hybrid' and has a unique classification code (20 or 21). To determine the length of shoreline for each shore type, the shoreline polyline files were projected with a projected coordinate system (PCS) chosen according to the state's metadata file. A new field was created in the attribute table of the newly projected polyline file and the 'calculate geometry' tool was used to determine the length (km) of each shoreline segment.

The shoreline polyline file was then projected with a detailed county polygon file available from ESRI for ArcMap 10.0. Shorelines falling along or within each coastal county were converted to polyline geodatabase files for each county. This process could not be automated due to geographic discrepancies between the shoreline polyline and the county polygon. Instead, these discrepancies were resolved on a case-by-case basis to ensure assignment of shoreline to the correct county and to avoid unassigned shoreline segments. For the Pacific and Atlantic coasts, the shoreline was then further subdivided into "open" shoreline or "sheltered" based on the type of water body along which the shoreline was located. We then calculated the total shoreline length (km), total hardened shoreline length, and percent of hardened shore for each county. Because many states have not updated their ESI files in the last five years, our shoreline hardening estimates are likely conservative (Table 2.A1). Our estimates of the percentage of shoreline hardening are within 3% of the estimates of hardened shoreline available from independent sources (Dugan et al. 2011, NC Division of Coastal Management 2012).

CVI data for regression tree analyses

We used the U.S. Geological Survey (USGS) Coastal Vulnerability Index (CVI) data for our regression tree analyses. The USGS CVI data were assembled using horizontal resolution resampled to a 3-minute grid cell, with a data set for each risk variable then linked to each grid point. For mapping purposes, data stored in the 3-minute grid were transferred to a 1:2,000,000 vector shoreline with each segment of shoreline lying within a single grid cell (Hammer-Klose and Thiehler 2001). Because the resolution for the CVI data was lower than the resolution for the ESI shoreline data, we were unable to assign a CVI value to each length of ESI shoreline. Instead, we divided the CVI data for each coastline by coastal county. The CVI data did include all coastal counties with sheltered shoreline (a majority of the Pacific sheltered coastal counties), as USGS mapped only those shorelines along the open coast and select major estuarine waterbodies (e.g., Chesapeake Bay). We then calculated the weighted average for each CVI factor based on the length of each CVI polyline segment.

Appendix References

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- National Oceanographic and Atmospheric Administration of the United States [NOAA]. 2013. National Coastal Population Report. NOAA State of the Coasts.
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 Table 2.A1. ESI data source origination year

State	Year
Alabama	2007
California	2006 (central), 2008 (northern), 1998 (San Francisco Bay), 2010 (southern)
Connecticut	2001
Delaware	1996
Florida	1995-1997
Georgia	1997
Louisiana	2003
Maine	2007 (habitat) 2009 (bluffs)
Maryland	2007
Massachusetts	2001
Mississippi	2010
New Hampshire	2004
New Jersey	1996 (Delaware Bay), 2001 (New York metropolitan area)
New York	2009 (Long Island), 2001 (New York metropolitan area), 2003 (Hudson River)
North Carolina	2011
Oregon	1985 (outer coast), 2004 (Columbia River)
Pennsylvania	1996
Rhode Island	2001
South Carolina	1996
Texas	1995
Virginia	2005
Washington	1985 (outer coast), 2006 (Puget Sound)

Table 2.A2. Shoreline ty	pe classification codes.	ESI codes and shore type	s courtesy of NOAA OR&R.

New		
Code	ESI Code	Shore Type
1	8C	Sheltered riprap
2	6B, 6D	Riprap, boulder rubble
3	1B	Exposed, solid man-made structures
4	8B	Sheltered, solid man-made structures
5	10C	Swamps
6	1C, 3B	Exposed rocky cliffs with boulder talus base
7	3A, 4, 5, 6A	Beaches (all grainsizes)
8	10A	Salt and brackish marshes
9	10B	Freshwater marshes
10	2A, 2B	Exposed wave-cut platforms, scarps, and steep slopes in bedrock, mud, or clay
11	7, 9A, 9C	Exposed tidal flats, sheltered tidal flats, hypersaline tidal flats
12	1A, 8A, 8D	Exposed or sheltered rocky shores, scarps in bedrock, mud, or clay
13	8F, 9B	Vegetated low banks
14	8E	Peat shorelines
15	10D	Scrub-shrub wetlands, mangroves
16	10E	Inundated low-lying tundra
20	6B+1B	Exposed hybrid structure
21	8B+8C	Sheltered hybrid structure

State	Hardened Sheltered Shoreline (km)	Sheltered Shoreline (km)	Hardened Sheltered Shoreline (%)	Hardened Open Shoreline (km)	Open Shoreline (km)	Hardened Open Shoreline (%)	Hardened Shoreline (km)	Total Shoreline (km)	Hardened Shoreline (%)	1970-2010 Percent Historic Population Change ^b	2010-2020 Projected Population Change ^b	Open coast ban (years) ^c	Sheltered coast ban (years) ^c
Atlantic													
СТ	477	1,907	25	0	0		477	1,907	25	18	5	0	0
DL	287	2,163	13	5	45	11	292	2,208	13	64	10	0	0
DC	29	54	53	0	0		29	54	53	-20	1	0	0
FLª	2,694	11,365	24	58	628	9	2,752	11,992	23	165	16	0	0
GA	92	6,340	1	14	158	9	106	6,498	2	82	19	0	0
ME	366	6,103	6	136	2,258	6	502	8,362	6	49	-5	27	27
MD	2,032	12,467	16	1	52	2	2,033	12,519	16	37	10	0	0
MA	568	3,408	17	148	875	17	715	4,283	17	16	5	0	0
NH	24	319	8	19	38	49	43	357	12	100	13	0	0
NJ	1,339	7,244	18	41	229	18	1,380	7,473	18	21	4	0	0
NY	366	6,103	6	136	2,258	6	502	8,362	6	6	5	0	0
NC	1,071	12,291	9	3	514	1	1,074	12,805	8	92	10	29	0
PA	168	468	36	0	0		168	468	36	-16	0	0	0
RI	234	938	25	21	149	14	255	1,087	23	11	5	29	29
SC	144	9,615	2	32	308	11	177	9,923	2	127	23	26	0
VA	1,392	14,364	10	13	192	7	1,404	14,556	10	94	18	24	0
Gulf													
AL							356	2,606	14		11		
FLª							4,427	26,383	17	165	16	0	0
LA							353	3,305	11	23	10	0	0
MS							367	3,033	12	54	5	0	0
ТХ							1,886	9,612	20	107	16	37	0
Pacific													
CA	1,009	3,602	28	335	2,680	12	1,344	6,282	21	62	8	0	0
OR	151	2,659	6	8	702	1	159	3,361	5	53	9	37	0
WA	1,022	5,765	18	5	327	1	1,027	6,092	17	99	18	11	0

Table 2.A3. Shoreline hardening and population statistics by state

^a The total hardened shoreline for Florida is 7,719 km and the total shoreline of Florida is 38,875 km, therefore 19% of Florida's shoreline is hardened.

^b NOAA 2013.

^c Years since a ban on shoreline hardening was legally mandated by the state, determined from individual state legislation. Note that there are exemptions to the bans and they very from state to state

APPENDIX 4.A STUDY COMPARISONS

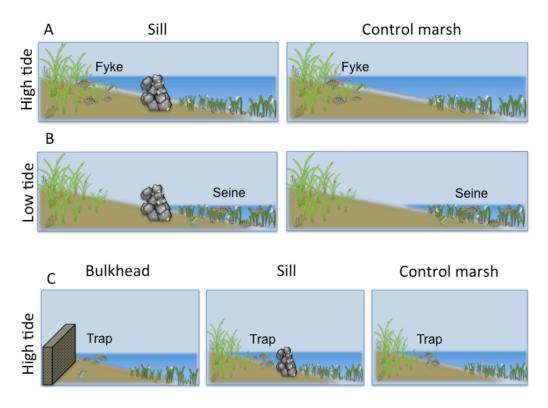


Figure 4.A1. Diagram of nekton sampling for a) fyke net sampling of inundated marsh during high tide at BACI and CI sill and control marsh sites; b) seine net sampling of subtidal seagrass and mudflat habitat during low tide at BACI and CI sill and control marsh sites; and c) minnow trap sampling of unvegetated edge habitat during high tide at bulkhead, CI sill, and CI control marsh sites. The CI sill and control marsh sites were sampled with all gear types (fyke and seine nets in 2010 and traps in 2011).



B



Figure 4.A2. Photo of a sill with a) drop-downs and b) gaps between the sill structures. Both designs were sampled in this study. Photos were taken on the flood tide at approximately 3 hours before high tide for (a) and 5 hours before high tide for (b).



Figure 4.A3. Photo of one of the PKS CI sills with a fyke net positioned to sample the marsh landward of the sill.

APPENDIX 4.B: RESULTS OF STATISTICAL ANALYSES

Table 4.B1. PERMANOVA results for fyke net community composition for each CI marsh sill and control site pair. Significant P values are in bold.

Response Variable	Source	DF	Sum of Squares	Mean Square	Pseudo F Ratio	Prob > F	Permutations
	Treatment	1	460.61	460.61	0.42	0.72	126
Fishes Pair 1	Error	8	8700.4	1087.6	0.12	0.72	120
	Treatment	1	2324.8	2324.8	2.76	0.01	126
Fishes Pair 2	Error	8	6749.7	873.72			
	Treatment	1	2364.6	2364.6	2.79	0.02	126
Fishes Pair 3	Error	8	6795.9	849.48			
	Treatment	1	904.47	904.47	1.14	0.3	126
Crustaceans Pair 1	Error	8	6364.4	795.54			
	Treatment	1	1963.7	1963.7	5.92	0.02	126
Crustaceans Pair 2	Error	8	2651.5	331.44			
	Treatment	1	1557.4	1557.4	4.18	0.025	91
Crustaceans Pair 3	Error	8	2983.2	372.9			

Table 4.B2. Matched pairs two-tailed t-test results for seine net catches for each CI marsh sill and control site pair.

Response Variable	DF	t-ratio	Prob > t
Individual fish per seine net set	14	-1.67	0.12
Grams fish per seine net set	14	-1.78	0.1
Individual crustaceans per seine net set	14	-0.01	0.99
Grams crustaceans per seine net set	14	-0.36	0.74

			Sum of			Prob >	
Response Variable	Source	DF	Squares	Mean Square	Pseudo F Ratio	F	Permutations
	Treatment	1	803.73	803.73	0.51	0.75	126
Fishes Pair 1	Error	8	12725	1590.6			
	Treatment	1	756.51	756.51	0.53	0.63	126
Fishes Pair 2	Error	8	11492	1436.5			
	Treatment	1	753.61	753.61	0.56	0.75	126
Fishes Pair 3	Error	8	10854	1356.8			
	Treatment	1	1267.1	1267.1	0.69	0.49	126
Crustaceans Pair 1	Error	8	14621	1827.6			
	Treatment	1	4347.5	4347.5	1.99	0.09	126
Crustaceans Pair 2	Error	8	17468	2183.5			
	Treatment	1	181.43	181.43	0.3	0.83	462
Crustaceans Pair 3	Error	8	5384.1	598.23			

Table 4.B3. PERMANOVA results for seine net community composition for each CI marsh sill and control site pair.

Region	Gear	Response Variable	Source	D F	Sum of Squares	Mean Square	F or t Ratio	Prob > F or t
		•	Model	3	9.12	3.04	2	0.15
			Treatment	1			-1.18	0.26
		Individual fish per set	Time Treatment X	1			2.06	0.06
			Time	1			-0.59	0.56
			Error	16	24.29	1.52		
			Model	3	11.94	3.98	1.42	0.27
			Treatment	1			-0.82	0.43
	Grams fish per set	Time Treatment X	1			1.11	0.28	
		Time	1			-1.54	0.14	
Hatteras	Frror	16	44.82	2.8				
Tratteras	I YKC		Model	3	0.72	0.24	0.15	0.92
			Treatment	1			-0.23	0.81
		Individual crustaceans per set	Time Treatment X	1			0.53	0.61
			Time	1			-0.36	0.72
			Error	16	25.16	1.57		
			Model	3	20.42	6.81	1.44	0.27
			Treatment	1			-0.46	0.65
		Grams crustaceans per set	Time Treatment X	1			2.01	0.06
			Time	1			0.26	0.79
			Error	16	75.66	4.73		

Table 4.B4. Two-factor ANOVA results for fyke net and seine net catches for each BACI marsh sill and control site pair. Significant P values are in bold.

			Model	3	32.38	10.79	6.84	0.004
			Treatment	1			-0.39	0.7
		Individual fish per set	Time Treatment X	1			4.5	0.0004
			Time	1			0.31	0.76
			Error	16	25.23	1.58		
			Model	3	35.03	11.68	4.49	0.02
			Treatment	1			-2.15	0.05
		Grams fish per set	Time Treatment X	1			2.98	0.01
	Hatteras Seine		Time	1			-0.05	0.96
Hatteras			Error	16	41.6	2.6		
Tratteras	Cente		Model	3	12.01	4	1.72	0.2
			Treatment	1			1.03	0.32
		Individual crustaceans per set	Time Treatment X	1			1.94	0.07
			Time	1			-0.57	0.58
			Error	16	37.25	2.33		
			Model	3	15.51	5.17	1.39	0.28
			Treatment	1			0.32	0.75
		Grams crustaceans per set	Time Treatment X	1			1.91	0.07
			Time	1			-0.64	0.53
			Error	16	59.7	3.73		

			Model	3	2124.72	708.24	2.22	0.11
			Treatment	1			0.43	0.67
		Individual fish per set	Time Treatment X	1			-2.43	0.02
			Time	1			0.84	0.41
			Error	24	7667.96	319.5		
			Model	3	226982.6	75661	0.58	0.63
			Treatment	1			-0.61	0.55
		Grams fish per set	Time Treatment X	1			-0.79	0.44
			Time	1			-1.01	0.32
Pine Knoll			Error	24	3106608.8	129442		
Shores	Fyke		Model	3	2.29	0.76	0.64	0.6
0			Treatment	1			-0.15	0.88
		Individual crustaceans per set	Time Treatment X	1			1.37	0.18
			Time	1			-0.14	0.89
			Error	24	28.8	1.2		
			Model	3	12.13	4.04	1.31	0.3
			Treatment	1			1.5	0.15
		Grams crustaceans per set	Time Treatment X	1			-0.55	0.58
			Time	1			1.55	0.14
			Error	24	74.28	3.1		

				Model	3	2.18	0.72	0.51	0.68
					3	2.10	0.72		
				Treatment	1			-1.13	0.27
			Individual fish per set	Time Treatment X	1			-0.42	0.68
				Time	1			-0.55	0.59
				Error	24	34.41	1.43		
				Model	3	25.54	5.51	3.61	0.03
				Treatment	1			-0.73	0.47
	Pine Knoll Se		Grams fish per set	Time Treatment X	1			3.15	0.004
				Time	1			0.38	0.71
		Seine		Error	24	56.71	2.36		
	Shores			Model	3	6.58	2.19	1.21	0.33
				Treatment	1			-1.53	0.14
			Individual crustaceans per set	Time Treatment X	1			-0.94	0.36
				Time	1			-1.04	0.31
				Error	24	43.66	1.82		
				Model	3	7.77	2.59	0.89	0.46
				Treatment	1			0.56	0.58
			Grams crustaceans per set	Time Treatment X	1			1.42	0.17
				Time	1			0.72	0.48
				Error	24	69.97	2.92		

			Model	3	3.18	1.06	2	0.15
			Treatment	1			-1.71	0.11
		Individual fish per set	Time Treatment X	1			-1.46	0.16
			Time	1			-0.21	0.83
			Error	16	8.48	0.53		
			Model	3	0.86	0.29	0.47	
			Treatment	1			-1	0.33
		Grams fish per set	Time Treatment X	1			0.43	0.68
			Time	1			-0.04	0.97
Swansboro	Fyke		Error	16	9.71	0.61		
Gwalisboro	Тукс	Individual crustaceans per set	Model	3	1.34	0.45	0.32	0.81
			Treatment	1			-0.66	0.52
			Time Treatment X	1			-0.58	0.57
			Time	1			0.68	0.51
			Error	16	22.06	1.38		
			Model	3	14.65	4.88	0.98	0.43
			Treatment	1			-0.91	0.38
		Grams crustaceans per set	Time Treatment X	1			-1.19	0.25
			Time	1			1.13	0.28
			Error	16	80.14	5.01		

				Model	3	1	0.33	0.58	0.64
				Treatment	1			-0.41	0.69
			Individual fish per set	Time Treatment X	1			-0.35	0.73
				Time	1			-0.94	0.36
				Error	16	9.21	0.58		
				Model	3	0.89	0.3	0.49	0.69
				Treatment	1			-1.04	0.32
	Swansboro S		Grams fish per set	Time Treatment X	1			0.04	0.97
				Time	1			-0.17	0.86
		Seine		Error	16	9.63	0.6		
	Swallsbord			Model	3	1.82	0.61	0.75	0.54
				Treatment	1			-0.92	0.37
			Individual crustaceans per set	Time Treatment X	1			-0.99	0.34
				Time	1			-0.23	0.82
				Error	16	12.91	0.81		
				Model	3	17.4	5.8	1.5	0.25
				Treatment	1			-1.52	0.15
			Grams crustaceans per set	Time Treatment X	1			-0.72	0.48
				Time	1			-0.58	0.57
				Error	16	61.68	3.85		

			Model	3	2.65	0.88	1.9	0.16
			Treatment	1			0.52	0.61
		Individual fish per set	Time Treatment X	1			-2.25	0.03
			Time	1			-0.46	0.65
			Error	22	10.27	0.47		
			Model	3	6.93	2.31	4.07	0.02
			Treatment	1			1.36	0.19
		Grams fish per set	Time Treatment X	1			-3.12	0.01
			Time	1			0.21	0.65
Holly Ridge	Fyke		Error	22	12.5	0.57		
Thony Triage	T yite		Model	3	1.62	0.54	0.58	0.63
			Treatment	1			0.17	0.87
		Individual crustaceans per set	Time Treatment X	1			0.41	0.68
			Time	1			-1.17	0.25
			Error	22	20.41	0.93		
			Model	3	5.21	1.74	1.81	0.17
			Treatment	1			2.13	0.04
		Grams crustaceans per set	Time Treatment X	1			-0.06	0.96
			Time	1			-0.42	0.68
			Error	22	21.1	0.96		
			Model	3	0.47	0.16	0.19	0.9
			Treatment	1			0.29	0.78
Holly Ridge	Seine	Individual fish per set	Time Treatment X	1			0.47	0.64
, J*			Time	1			-0.43	0.67
			Error	22	18.25	0.83		
		Grams fish per set	Model	3	1.69	0.56	0.82	0.5

	Treatment	1			-0.35	0.73
	Time	1			1.52	0.14
	Treatment X					
	Time	1			0.08	0.93
	Error	22	15.12	0.69		
	Model	3	3.37	1.12	0.41	0.75
	Treatment	1			-0.74	0.47
Individual crustaceans per set	Time	1			-0.69	0.5
	Treatment X					
	Time	1			0.28	0.78
	Error	22	59.92	2.72		
	Model	3	3.18	1.06	0.23	0.88
	Treatment	1			0.04	0.97
Grams crustaceans per set	Time	1			-0.1	0.92
	Treatment X					
	Time	1			0.8	0.43
	Error	22	103.18	4.69		

Region	Gear	Response Variable	Source	DF	Sum of Squares	Mean Square	Psuedo F	Prob > F	Permutations
			Treatment	1	4281.5	4281.5	1.74	0.13	9951
		Individual	Time Treatment X	1	7885.5	7885.5	3.21	0.00	9935
		fishes per set	Time	1	2304.6	2304.6	0.94	0.51	9948
	Fyke		Error	14	34394.0	2456.7			
	Гуке		Treatment	1	2246.5	2246.5	1.90	0.20	9972
		Individual crustacean	Time Treatment X	1	734.4	734.37	0.62	1	9963
		species per set	Time	1	1602.6	1602.6	1.36	0.30	9961
Hatteras			Error	13	15359.0	1181.4			
Tratteras			Treatment	1	4213.5	4213.5	1.57	0.16	9940
		Individual fishes per set	Time Treatment X	1	5970.6	5970.6	2.23	0.04	9926
		lisiles per set	Time	1	2232.4	2232.4	0.83	0.56	9940
	Seine		Error	16	42854.0	2678.4			
	Jeine		Treatment	3	1687.5	1687.5	1.48	0.27	9966
		Individual crustacean	Time Treatment X	1	4512.1	4512.1	3.96	0.04	9960
		species per set	Time	1	425.4	425.4	0.37	0.69	9955
			Error	1	14795.0	1138.1			

Table 4.B5. Two-factor PERMANOVA results for fyke net and seine net community composition for each BACI marsh sill and control site pair. Significant P values are in bold.

			Treatment	1	1126.7	1126.7	0.79	0.60	9951
		Individual	Time Treatment X	1	5143.8	5143.8	3.62	0.00	9940
		fishes per set	Time	1	992.3	992.3	0.70	0.67	9950
	Fyke		Error	24	34075.0	1419.8			
	Туке		Treatment	1	325.0	325.0	0.28	0.74	9969
		Individual crustacean	Time Treatment X	1	728.8	728.8	0.62	0.54	9968
		species per set	Time	1	304.5	304.5	0.26	0.74	9966
Pine Knoll Shores			Error	24	28268.0	1177.8			
		Individual fishes per set	Treatment	1	1268.9	1268.9	0.89	0.51	9955
			Time Treatment X	1	2643.7	2643.7	1.86	0.10	9945
			Time	1	516.1	516.1	0.36	0.88	9948
	Seine		Error	21	29871.0	1422.4			
	Ocific		Treatment	1	1380.6	1380.6	1.08	0.37	9960
		Individual crustacean	Time Treatment X	1	10100.0	10100.0	7.93	0.00	9956
		species per set	Time	1	603.3	603.3	0.47	0.70	9960
			Error	20	25464.0	1273.2			

			Treatment	1	3532.1	3532.1	2.29	0.05	9948
		Individual	Time Treatment X	1	3211.3	3211.3	2.08	0.07	9959
		fishes per set	Time	1	1105.2	1105.2	0.72	0.64	9953
	Fyke		Error	16	24725.0	1545.3			
	Гуке		Treatment	1	157.1	157.1	0.17	0.78	9961
		Individual crustacean	Time Treatment X	1	108.3	108.3	0.12	0.81	9953
		species per set	Time	1	132.5	132.5	0.14	0.80	9966
Swansboro			Error	16	12001.0	923.1			
Gwalisboro		Individual	Treatment	1	525.6	525.6	0.37	0.84	9937
			Time Treatment X	1	1690.4	1690.4	1.19	0.33	9952
		fishes per set	Time	1	666.2	666.2	0.47	0.77	9952
	Seine		Error	16	22764.0	1422.7			
	Ocific		Treatment	1	1858.3	1858.3	1.19	0.32	9950
		Individual crustacean	Time Treatment X	1	2172.9	2172.9	1.39	0.27	9967
		species per set	Time	1	1332.9	1332.9	0.85	0.40	9952
			Error	11	17246.0	1567.8			

			Treatment	1	3244.9	3244.9	2.45	0.02	9950
		Individual	Time Treatment X	1	2523.2	2523.2	1.91	0.07	9945
		fishes per set	Time	1	-225.0	-225.0	Negative		
	Fyke		Error	22	29098.0	1322.7			
	Туке		Treatment	1	446.6	446.6	1.30	0.26	9950
		Individual crustacean	Time Treatment X	1	274.8	274.8	0.80	0.46	9952
		species per set	Time	1	484.6	484.6	1.41	0.24	9943
Holly Ridge			Error	22	7573.7	344.3			
Tiony Triage		Individual	Treatment	1	1549.3	1549.3	1.33	0.26	9944
			Time Treatment X	1	555.8	555.8	0.48	0.81	9947
		fishes per set	Time	1	877.3	877.3	0.75	0.61	9948
	Seine		Error	20	23327.0	1166.3			
	Genie		Treatment	1	242.6	242.6	0.16	0.81	9956
		Individual crustacean	Time Treatment X	1	427.1	427.1	0.27	0.73	9962
		species per set	Time	1	5619.2	5619.2	3.61	0.06	9953
			Error	19	29541.0	1554.8			

Table 4.B6. Nested ANOVA	results for trap catches.	. Significant P values are in bold.

			Variance	Variance	F	Prob >
Response Variable	Source	DF	Ratio	Component	Ratio	F
	Treatment Site	2			8.75	0.02
	[Treatment]		-0.10	-0.18		
Individual fish per set	Error		1.83	0.43		
	Treatment Site	2			5.38	0.04
	[Treatment]		-0.04	-0.12		
Grams fish per set	Error		3.02	0.71		
	Treatment Site	2			1.49	0.38
	[Treatment]		0.08	0.03		
Individual crustaceans per set	Error		0.37	0.09		
	Treatment Site	2			0.05	0.95
	[Treatment]		0.05	0.03		
Grams crustaceans per set	Error		0.74	0.18		

Response	-		Sum of	Mean	Pseudo F	Prob >	
Variable	Source	DF	Squares	Square	Ratio	F	Permutations
	Treatment	2.00	2.61	1.30	5.39	0.04	5544
	Site [Treatment]	6.00	1.48	0.25	6.90	0.00	9951
Bivalves	Error	87.00	3.10	0.04			
	Treatment	2.00	8.00	4.00	6.56	0.04	476
	Site [Treatment]	6.00	3.73	0.62	9.08	0.00	9942
Barnacles	Error	87.00	5.96	0.07			
	Treatment	2.00	0.08	0.04	4.25	0.01	29
	Site [Treatment]	6.00	0.06	0.01	6.55	0.00	9954
Other	Error	87.00	0.13	0.00			

Table 4.B7. Nested PERMANOVA results for epibiota. Significant P values are in bold.