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Ribbed mussel *Geukensia demissa* population response to living shoreline design and ecosystem development

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Abstract. Coastal communities increasingly invest in natural and nature-based features (e.g., living shorelines) as a strategy to protect shorelines and enhance coastal resilience. Tidal marshes are a common component of these strategies because of their capacity to reduce wave energy and storm surge impacts. Performance metrics of restoration success for living shorelines tend to focus on how the physical structure of the created marsh enhances shoreline protection via proper elevation and marsh plant presence. These metrics do not fully evaluate the level of marsh ecosystem development. In particular, the presence of key marsh bivalve species can indicate the capability of the marsh to provide non-protective services of value, such as water quality improvement and habitat provision. We observed an unexpected low to no abundance of the filter-feeding ribbed mussel, *Geukensia demissa*, in living shoreline marshes throughout Chesapeake Bay. In salt marsh ecosystems along the Atlantic Coast of the United States, ribbed mussels improve water quality, enhance nutrient removal, stabilize the marsh, and facilitate long-term sustainability of the habitat. Through comparative field surveys and experiments within a chronosequence of 13 living shorelines spanning 2–16 years since construction, we examined three factors we hypothesized may influence recruitment of ribbed mussels to living shoreline marshes: (1) larval access to suitable marsh habitat, (2) sediment quality of low marsh (i.e., potential mussel habitat), and (3) availability of high-quality refuge habitat. Our findings suggest that at most sites larval mussels are able to access and settle on living shoreline created marshes behind rock sill structures, but that most recruits are likely not surviving. Sediment organic matter (OM) and plant density were correlated with mussel abundance, and sediment OM increased with marsh age, suggesting that living shoreline design (e.g., sand fill, planting grids) and lags in ecosystem development (sediment properties) are reducing the survival of the young recruits. We offer potential modifications to living shoreline design and implementation practices that may facilitate self-sustaining ribbed mussel populations in these restored habitats.

Key words: Chesapeake Bay; ecological engineering; ecosystem services; *Geukensia demissa*; living shorelines; ribbed mussel.

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INTRODUCTION

The potential for natural infrastructure to protect coasts by slowing erosion and reducing storm surge and flooding can be considerable in many settings, particularly in areas subject to high relative rates of sea level rise and vulnerability to storms (Arkema et al. 2013, Sutton-Grier et al. 2015, Narayan et al. 2016). Natural features that can attenuate waves (e.g., marshes) are being created to protect shorelines in many estuaries and coasts, and this practice has grown substantially over the past 20 yr (Sutton-Grier et al. 2015). When used for shore protection, these created features (living shorelines henceforth) often involve a combination of green-gray (hybrid) infrastructure, specifically restoring or creating a fringing marsh in combination with a stabilizing sill structure placed offshore and parallel to the marsh (Bilkovic et al. 2017a), which can be very effective at erosion protection (Shepard et al. 2011, Gittman et al. 2014, Morris et al. 2019, Fig. 1) and more resilient than armoring (e.g., bulkheads) to storm events and sea level rise (Gittman et al. 2014, Smith et al. 2017, Mitchell and Bilkovic 2019). Living shorelines are being valued for not only protective services (e.g., wave energy reduction, mitigating storm surge impacts), but also non-protective services and co-benefits including water quality improvement, nutrient removal, and habitat provision (e.g., Sutton-Grier et al. 2015, Gittman et al. 2016, Beck et al. 2017).

As with any created or restored habitat, a created marsh can take years to decades to approach functional equivalency in providing similar levels of ecosystem services with a reference habitat (Craft et al. 2003). The fringing marshes created as part of a living shoreline project appear to be following similar trajectories as other created marsh types, even though the construction practices vary. Marsh plant density and biomass tend to become similar to reference marshes within a few years (but see Bilkovic and Mitchell 2017) as does fish utilization (Gittman et al. 2016), while some secondary productivity measures (e.g., benthic invertebrate species abundance, diversity) and soil development (e.g., organic matter content) tend to take much longer (>10 yr; Currin et al. 2008, Bilkovic and Mitchell 2013, 2017. Bilkovic et al. 2016, Beck et al. 2017,

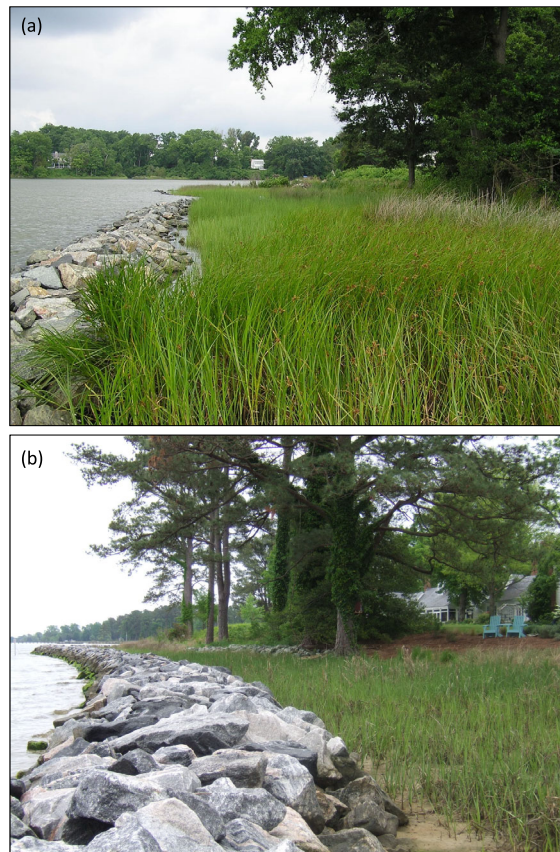


Fig. 1. (a) Living shoreline approach with a created marsh and stabilizing sill structure to encourage marsh establishment. The use of marshes and sills or breakwaters is now a commonly practiced nature-based approach to shore protection along the East and Gulf Coasts of the United States. (b) Prominent sill structure that dominates the living shoreline and may inhibit access to the marsh for some marsh fauna. Photo credits: Karen Duhring, Center for Coastal Resources Management (CCRM), Virginia Institute of Marine Science (VIMS).

Chambers et al. 2020). The successful creation of a salt marsh ecosystem may be discernible by key components, including native marsh biota from several principal faunal groups including intertidal bivalves (*Geukensia* spp.), marine crabs (*Uca* spp., *Callinectes* spp.), marine snails (*Littorina* spp.), marsh fish (*Fundulus* spp.), estuarine turtles (*Malaclemys terrapin*), and marsh birds (e.g., *Ammodramus caudacutus* saltmarsh sparrow); species assessments can be used as performance indicators for marsh restoration efforts.

Geukensia demissa (ribbed mussel) is a key bivalve species in salt marshes that enhances marsh resilience (Bertness et al. 2015, Derksen-Hooijberg et al. 2019), nitrogen removal (Jordan and Valiela 1982, Galimany et al. 2017, Bilkovic et al. 2017b, Isdell 2018), and water and habitat quality (Ward and Shumway 2004, Angelini et al. 2015, Isdell 2018, Kreeger et al. 2018). Ribbed mussels actively manipulate their habitat, fundamentally influencing the productivity of the marsh through their mutualistic relationship with *Spartina alterniflora* (cordgrass henceforth). Specifically, mussels aggregate around cordgrass stems (Nielsen and Franz 1995) where they attach to substrate with byssal threads, stimulate root and rhizome growth with biodeposits, and bind sediment, thereby increasing plant height, stabilizing the marsh, and reducing erosion (Bertness 1984). In turn, high-density cordgrass serves as predator and/or heat stress refuge for mussels (Angelini et al. 2015). Ribbed mussels are also efficient filter feeders, removing large amounts of particulate material from overlying waters thereby enhancing water clarity (Kreeger and Newell 2001, Galimany et al. 2017). This augments pelagic-benthic coupling processes by transferring and concentrating nitrogen and carbon from the water column to the marsh sediments where nutrients become available for microbial processes including denitrification (Jordan and Valiela 1982).

Ribbed mussel larvae are planktonic, typically spending about 2–3 weeks in open water before settling within a salt marsh (Virgin et al. 2019), although laboratory studies performed in Connecticut, USA, have demonstrated their ability to remain in suspension for up to 6 weeks (Loosanoff and Davis 1963). In most large tidal creeks and rivers, existing mussel populations are likely not limited by larval supply; however, hydrodynamic flows can result in some marsh habitat serving as sources and others acting as sinks for bivalve populations (Turley et al. 2019). Recruitment success is not only dependent on a larval source, but also on habitat suitability and post-settlement survivorship. The combination of hydrodynamics and site characteristics can result in highly localized differences (Chesson 1998). Thus, the habitat characteristics of a salt marsh and the larval dispersal pathways contribute to the status of mussel populations.

Larval ribbed mussel settlement is facilitated by the presence and density of cordgrass along marsh edges. Acting as baffles, the cordgrass stems slow the flow of the water over the marsh surface which allows large particles (and competent-to-settle mussel larvae) to settle onto the marsh surface (Leonard and Croft 2006). Once settled and metamorphosed from planktonic to benthic forms (i.e., the reabsorption of the veliger), young mussels will use their muscular foot to crawl along the marsh surface to find a suitable microclimate (e.g., the moist, protected crevices among clumps of adult mussels, or nestled into the cordgrass root mats under their shady canopy of leaves; Nielsen and Franz 1995). Once found, they anchor themselves into position using byssal threads. If no suitable microclimate can be found, small mussels may also cast out a tuft of byssus to function as a drogue net allowing them to temporarily reenter the plankton to seek a better home (Baker and Mann 1997). Living in the intertidal zone, ribbed mussel recruits must strike a difficult balance between maximizing submergence time and predator avoidance. Ribbed mussels are most likely to thrive in areas that reduce desiccation stress (lower in the tidal frame in sediments that retain moisture under the shade of cordgrass), maximize feeding opportunities (also lower in the tidal frame and closer to the front (waterward edge) of the marsh), and lower predation pressure (in and among clumps of adult conspecifics and cordgrass roots). These factors culminate in the typical density profiles observed for ribbed mussels throughout their range, that is, high mussel density on the front edge of the marsh, and decreased density with perpendicular distance up and into the marsh (Bertness and Grosholz 1985, Nielsen and Franz 1995, Isdell et al. 2018, Moody and Kreeger 2020).

Here, we comparatively assess ribbed mussel distribution and abundance within created living shoreline marshes and paired natural fringing marshes in Chesapeake Bay. Further, we explore possible reasons for limited ribbed mussel recruitment (defined here to include settlement and post-settlement survival to reproduction) in living shoreline marshes. We used fundamental understandings of the life history and functional role of ribbed mussels within the salt marsh community to develop and test hypothesized reasons

for limited recruitment. Specifically, we investigated the potential relationship between mussel settlement and survival in hybrid living shorelines with respect to three factors: (1) larval access to suitable marsh habitat, (2) sediment quality in the marsh, and (3) availability of high-quality refuge habitat. These factors were selected for our assessment because they have been linked to ribbed mussel recruitment in marshes (e.g., Seed 1969, Bertness 1984, Bertness and Grosholz 1985, Jost and Helmuth 2007, Jenewein and Gosselin 2013), and/or they may vary in living shoreline marshes due to construction practices, such as planting spacing or sediment fill characteristics (e.g., O'Donnell 2016, Bilkovic and Mitchell 2017). We acknowledge that the factors presented are likely not mutually exclusive; multiple factors may interact to influence ribbed mussel recruitment in a living shoreline marsh and the factors determining mussel presence may differ by location or living shoreline design. We then propose strategies to increase ribbed mussel recruitment in living shoreline marshes toward self-sustaining ribbed mussel populations in restored habitats.

METHODS

Ribbed mussel abundance and distribution

Ribbed mussel density was measured in a chronosequence of hybrid living shorelines (created fringing marshes) spanning 2–16 yr in age (years since construction) and compared with paired natural fringing marshes in the southern Chesapeake Bay (Fig. 2). From an initial candidate pool of more than 100 living shorelines with similar design features (created marsh, sand fill, and rock sill) that was extracted from the Virginia Wetlands Permit Database (CCRM 2017), 13 sites were selected on the basis of (1) presence and accessibility of a paired natural fringing marsh within close proximity (separation distance was 395 m on average) and with similar environmental conditions (e.g., exposure, land use, salinity), (2) property-owner permissions, and (3) age of project (minimum of 2 yr old to allow plant establishment and inclusion of a range of ages). The sites sampled represented a range of landscape settings (i.e., dominant surrounding land use of agricultural, developed, or natural (i.e., forest, open space)

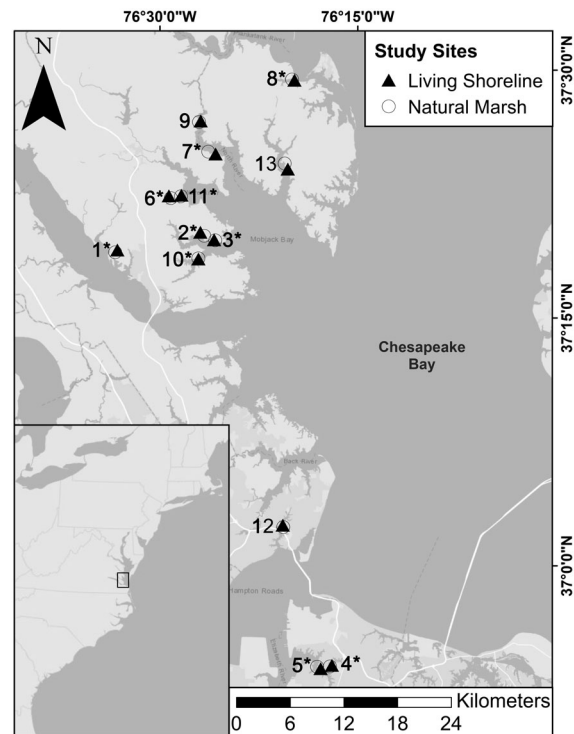


Fig. 2. Locations of a chronosequence of 13 paired living shoreline (LS) and natural fringing marshes (NM) that were surveyed to determine ribbed mussel abundance, cordgrass density, and sediment characteristics. In addition, mussel recruitment studies were conducted at 10 of the living shorelines sites (marked with an asterisk).

within a 1 km radius) that is characteristic of Chesapeake Bay watershed (Table 1). Living shoreline and paired natural marsh sites ($n = 13$ pairs) were sampled during fall (September–October) 2018 at the end of the marsh plant growing season; paired sites were sampled concurrently to ensure similar environmental conditions. At each site, we surveyed 6 random transects that ran perpendicular to the seaward edge of the marsh. Within the low marsh (cordgrass dominated) area, we placed two 0.25 m² quadrats along each transect at 1-m intervals representing distances of 0–1 and 1–2 m from the seaward edge and we counted the number of adult and juvenile (<25 mm) mussels and cordgrass stems in each quadrat. Previous work within Chesapeake Bay marshes has shown that the vast majority of mussels (~85%) are found within 2 m of the seaward

Table 1. Living shoreline and natural marsh properties.

Pair	Type	Age (y)	Land cover	Shl armor (%)	Distance to nearest marsh (m)	Inundation (hrs/mo)	Cordgrass density (#/m ²)	Sill height above MHW (cm)	Mussel density (#/m ²)
1	LS	7	Mix	3%	6.8	146.7	92.0 ± 39.0	14.5	3.3 ± 7.2
1	NM		Mix	4%	5.2	285.3	154.3 ± 101.6		144.0 ± 219.8
2	LS	4	Mix	11%	6.7	165.7	130.7 ± 47.0	9	1.0 ± 3.5
2	NM		Mix	7%	5.5	111.1	309.0 ± 115.8		262.3 ± 302.5
3	LS	2	Nat	0%	3.6	265.1	124.7 ± 62.7	0	0.0 ± 0.0
3	NM		Nat	0%	3.5	259.4	223.3 ± 83.0		77.3 ± 102.0
4	LS	7	Dev	44%	11.2	141.4	228.0 ± 92.9	0	28.3 ± 21.1
4	NM		Dev	51%	14.2	97.9	354.7 ± 206.6		212.3 ± 165.8
5	LS	10	Dev	62%	28.7	93.6	110.7 ± 93.7	7.2	29.0 ± 22.7
5	NM		Dev	62%	33.9	84.1	151.7 ± 86.9		31.0 ± 57.2
6	LS	9	Mix	12%	5.4	142.1	111.7 ± 27.5	5.5	5.3 ± 7.9
6	NM		Mix	15%	5.8	209.0	159.0 ± 84.4		28.7 ± 41.6
7	LS	12	Mix	15%	8	152.8	377.5 ± 125.0	0	91.6 ± 89.7
7	NM		Mix	21%	6.9	159.4	153.7 ± 36.2		55.0 ± 52.2
8	LS	7	Mix	20%	28.4	110.9	109.0 ± 98.2	0.8	0.0 ± 0.0
8	NM		Mix	22%	25	198.9	47.0 ± 63.2		56.7 ± 82.1
9	LS	3	Mix	6%	4.2	211.7	94.0 ± 31.6	23.3	0.0 ± 0.0
9	NM		Mix	6%	4.3	185.4	160.4 ± 52.2		29.8 ± 44.1
10	LS	16	Nat	12%	4	224.7	252.7 ± 78.0	0	38.3 ± 39.5
10	NM		Nat	11%	3.8	18.1	30.3 ± 55.0		176.0 ± 127.7
11	LS	9	Mix	25%	8.7	343.9	206.0 ± 124.9	11	25.7 ± 40.5
11	NM		Mix	26%	8.6	268.9	356.0 ± 131.2		174.3 ± 148.4
12	LS	6	Dev	41%	29.5	299.7	186.7 ± 72.1	1.5	9.0 ± 31.2
12	NM		Dev	43%	35.9	190.2	101.3 ± 78.8		2.3 ± 5.8
13	LS	16	Mix	22%	14.5	289.4	98.0 ± 87.6	0	4.7 ± 10.9
13	NM		Mix	25%	13	228.9	169.0 ± 120.8		114.3 ± 186.2

Notes: Inundation period, mean *S. alterniflora* (cordgrass) and mussel density (\pm SD), and shoreline armoring and land cover surrounding each site. Living shoreline properties: Sill height above mean high water (MHW) and age (number of years since construction). Land cover within a 1 km radius of the site was classified into 3 major groups: developed (>60% developed and managed lands), natural (>75% natural lands—forest/tree/scrub-shrub), or mixed use (mix of pasture, cropland, developed, managed, and natural lands). Shoreline armor refers to the percent armoring (riprap revetment or bulkhead) within a 1 km radius of the site. Marsh habitat connectivity is represented as the average distance (along the shoreline) to nearest marsh.

edge (Bilkovic et al. 2017, Isdell et al. 2018). We averaged mussel densities across all quadrats ($N = 12$) for a given site and compared marsh types using paired t -tests. Prior to transect placement at living shorelines, sill characteristics, including length (m) along shore, height (m) above mean high water (MHW), and location of tidal openings, were assessed on-site. In most sites, a single sill structure (on average, 49 m [± 17 SD] long) fronted the marsh with tidal openings on either end of the rock sill; transects were placed behind the sill. Two sites had multiple (2–3) smaller sills (<30 m in length) fronting the marsh ($\sim 21 \pm 6$ m in length); at these sites, transects were placed behind 2 adjacent sills. Sill heights were on average 5.6 cm above mean high water (MHW). For each site, we also estimated the average distance (along the shoreline) to the

nearest marsh in ArcGIS Pro as a measure of landscape conditions that may influence mussel distribution (e.g., areas with shoreline armoring will result in disconnected landscapes that have longer distances between shoreline marshes).

To assess the effects of marsh type, cordgrass density, inundation duration (methods described below), and distance to nearest marsh on mussel densities, we ran a generalized linear regression with a negative binomial distribution and pair as a random factor using the integrated nested Laplace approximation (INLA) method (Rue et al. 2009).

Larval recruitment

To evaluate whether rock sills fronting living shoreline marshes may interfere with larval mussel access to suitable marsh habitat, during 2018,

we staked 6 plastic mesh dish-scouring pads (i.e., generic Tuffy pads) to the marsh surface behind the rock sill at 10 living shorelines (ranging from 2 to 16 yr post-construction) throughout Virginia (Fig. 2) to collect ribbed mussel recruits (see Arribas et al. 2015 for examples of the use of this settlement substrate in other mytilids). The pads were placed early in the spawning season (July) and collected near the end of the spawning season (October). Pads were visually inspected for the presence/absence of juvenile mussels.

Sediment quality

Sediment quality for ribbed mussels was evaluated by measuring sediment properties indicative of desiccation risk (soil moisture, organic matter, and grain size; Seed 1969, Jenewein and Gosselin 2013) or potential food sources for settling recruits (sediment chlorophyll *a*, Vaughn and Hakenkamp 2001). At each site, triplicate soil cores to 5 cm depth were collected within the lower marsh (dominated by cordgrass). For each core, sediment grain size, soil water content, and organic matter (OM) were determined using standard analytical methods and the top 0.5 cm of the cores was used to measure levels of sediment chlorophyll *a* following standard methods detailed in Arar and Collins (1997). Water content was calculated from weight loss after oven drying wet soil cores at 60°C. From dried samples, organic content was calculated from weight loss after ashing for 4 h at 450°C. Percentages of gravel, sand, silt, and clay in sediments were determined by standard wet sieve and pipette analysis (Folk 1980) at the Virginia Institute of Marine Science (VIMS) Analytical Services Center. The triplicate cores were averaged per site to obtain a mean sediment chlorophyll *a* (dry weight), percent soil water content, and percent OM, that were then compared between marsh type (living shorelines vs reference marshes) using one-tailed paired *t*-tests. For *t*-tests, we posited that OM, chl *a*, soil water content, and silt/clay would be lower in living shorelines than reference marshes because soil properties would not be fully developed. Conversely, the proportion of sand was posited to be higher in living shorelines than reference marshes. For living shorelines, we examined the relationship between sediment properties (percentages of soil water, OM, sand, and chl *a*),

living shoreline age, and mussel density using Spearman's rank correlation coefficient. Then, we used negative-binomial generalized linear regression in R (MASS v7.3-50) to independently examine the relationships between correlated ($r_s > 0.6$) sediment properties and mussel density.

Availability of high-quality refuge habitat

Habitat quality was evaluated by measuring cordgrass density and marsh inundation extent as indicators of refuge and feeding opportunities. During mussel surveys, cordgrass stems were counted within the same 0.25-m² quadrats used for mussel counts as described above. Cordgrass densities were then averaged across all low marsh quadrats ($N = 12$) for a given site and marsh types were compared using paired *t*-tests. The duration and extent of inundation of the marsh was estimated to determine the relative amount of low marsh habitat and feeding opportunities available to ribbed mussels. We estimated the distribution of tidal inundation across the marsh surface using the closest NOAA tidal predictions (https://tidesandcurrents.noaa.gov/tide_predictions.html) for each reference marsh and living shoreline pair for a one-month period of time (July 2018). Tidal predictions account for geographic variability in tide ranges between sites and are spatially interpolated from tide gauge data; it allows us to compare general conditions between marsh/living shoreline pairs, but is not an exact accounting of the experienced water levels over the sampling time period (e.g., storm tides are not included in the analysis). Tidal predictions are furnished as time and height of high and low tides; therefore, we had to interpolate between the high and low water to create a full tidal curve. A frequency analysis was used to calculate the exceedance period at 0.1-m increments for each site. Site elevations were obtained using a digital elevation model (DEM) derived from on-site elevation data collected using a stadia rod for elevation and a Trimble Geo 7× handheld GPS for latitude and longitude. At each site, the mean high water (MHW) line was visually demarcated as the transition between the low and high marsh vegetation from geo-rectified high-resolution drone imagery (DJI Mavic Pro) and referenced

to MHW from the tidal analysis. Hours of inundation were calculated for marsh elevations using the tidal analysis data and averaged across the low marsh surface for each site. For living shorelines, we examined the relationship between habitat features (cordgrass density, inundation), living shoreline age, and mussel density using Spearman's rank correlation coefficient. The age of the living shoreline marsh and the density of cordgrass were independently compared with ribbed mussel density using negative-binomial generalized linear regression in R (MASS v7.3-50).

RESULTS

Ribbed mussel abundance and distribution

Adult mussels were 4 times more dense in reference marshes (mean \pm SE, 82 ± 17 mussels/m²) than in living shoreline marshes (17 ± 7 mussels/m², $t_{(12)} = -3.544$, $P = 0.004$; Fig. 3). Similarly, juvenile mussels were found in very low densities, when present, in living shoreline marshes (1.1 ± 0.5 mussels/m²) compared with reference marshes (23.0 ± 6.8 mussels/m², $t_{(12)} = -3.146$, $P = 0.008$). Mean densities of mussels and cordgrass across all transects in living shorelines and natural marshes for the first two

meters into the marsh are provided in Appendix S1: Table S1. Mussel densities in the natural marsh exhibited the expected decline in density from the edge to the second meter of the marsh, whereas the mussel in the living shoreline had similar, low densities across the first two meters of the marsh. Cordgrass densities were similar across both the first two meters of marsh and between marsh types. The INLA regression identified that both marsh type ($\beta = 1.94$, 1.11–2.78; mean, 95% credible interval) and cordgrass density ($\beta = 0.62$, 0.23–1.06) had positive, non-zero effects on mussel density, while neither inundation duration ($\beta = -0.22$, -0.59 to 0.18) nor distance to nearest marsh ($\beta = -0.15$, -0.65 to 0.38) had an effect.

Larval recruitment

Ribbed mussel recruits were observed in settlement pads from all 10 sampled living shoreline marshes. Young mussels were observed even in sites where adults were absent (3 sites) or present in very low densities (<4 mussels/m²; 2 sites), indicating that larval mussels are capable of accessing the living shoreline marshes behind the sills.

Sediment quality

Living shoreline sediments tended to be coarser, drier, and less organic-rich than reference marshes. The moisture content of sediment from living shoreline marshes (mean percent of soil volume \pm SD, $41.5\% \pm 9.9$) was lower than reference marshes ($53.1\% \pm 10.3$; paired t -test, $t_{(12)} = -2.6$, $P = 0.01$). Likewise, living shoreline marsh sediment was coarser with less fines (91.9% sand, 8.0% silt/clay) and had less organic matter (2.6% OM) than reference marshes (82.1% sand, 17.9% silt/clay, 6.7% OM; paired t -tests, sand $t_{(12)} = 2.1$, $P < 0.03$; silt/clay $t_{(12)} = -2.1$, $P < 0.03$; OM $t_{(12)} = -3.1$, $P < 0.01$). Concentrations of chlorophyll *a* in living shoreline and reference marshes were similar (mean chl *a* \pm SD: 29.5 ± 14.9 ; 20.3 ± 15.5 $\mu\text{g/g}$, respectively; paired t -test, $t_{(12)} = 1.4$, $P = 0.9$). The living shorelines we surveyed ranged in age from 2 to 16 yr. Only soil OM in living shoreline marshes tended to increase with age ($r_s = 0.63$), but OM remained lower than reference marsh mean values (6.7%) regardless of age. Living shoreline OM increased at a rate of $0.187\% \text{ yr}^{-1}$, with an intercept of 1.012% (linear regression, adj-

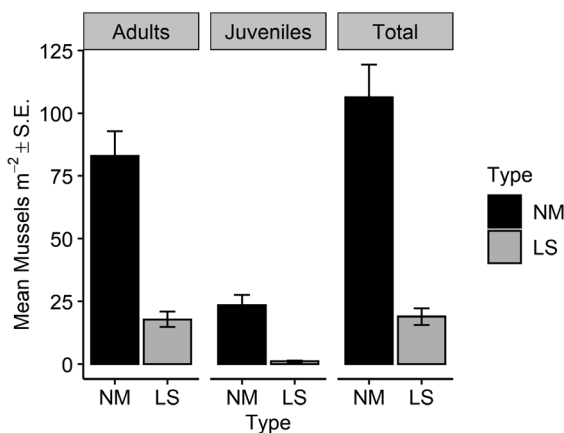


Fig. 3. Ribbed mussel abundance (adult, juvenile, total) within natural fringing marshes (NM) or the living shoreline marshes (LS). Juveniles were animals <25 mm. Living shorelines and natural fringing marshes were paired ($n = 13$ pairs); pairs were within close vicinity to one another with similar exposures. Sites were located throughout the lower Chesapeake Bay, Virginia (Fig. 2), and surveyed during 2018.

$R^2 = 0.19$). Ribbed mussel density increased with increasing OM (negative-binomial generalized linear regression, $z_{(11)} = 2.77$, $P = 0.006$).

Availability of high-quality refuge habitat

Higher density of saltmarsh cordgrass was correlated with higher mussel density for both living shorelines and paired reference marshes when mussels were present; mussels were absent at 3 living shoreline sites (Fig. 4b). Mussel density was higher at older, more established living shoreline marshes (negative-binomial generalized linear regression, $z_{(11)} = 3.8$, $P < 0.001$; Fig. 4a), and positively correlated with cordgrass density (Fig. 4b), although mussel density was still lower than observed in reference marshes. Saltmarsh cordgrass density was similar between living shoreline (163.2 ± 84.4 stems/m²) and natural marshes (182.3 ± 103.8 stems/m², $t_{(12)} = -0.529$, $P = 0.606$), and cordgrass density was not correlated with marsh age ($r_s = 0.26$). Relative calculated inundation period of the low marsh was not correlated with mussel density, and all of the living shorelines had relative inundation periods similar to or greater than the paired natural marshes.

DISCUSSION

Unexpectedly, we observed that ribbed mussels are often absent or in low abundance within living shoreline marshes in Chesapeake Bay, which may impede the ability of these marshes to provide expected ecosystem services (some of which are being ascribed a significant economic value, e.g., nitrogen removal for Total Maximum Daily Load credits; Wainger 2012). Our findings suggest that at most sites larval mussels are able to access and settle on living shoreline created marshes behind rock sill structures, but the low to no abundance of juvenile and adult mussels at these sites suggests that most recruits are likely not surviving. The primary factors examined that were correlated with mussel abundance were related to the quality of the marsh habitat (sediment organic matter and plant density) that may influence survival of the young mussels.

Larval access to suitable marsh habitat

The size and height above mean high water of living shoreline sills vary between projects, based

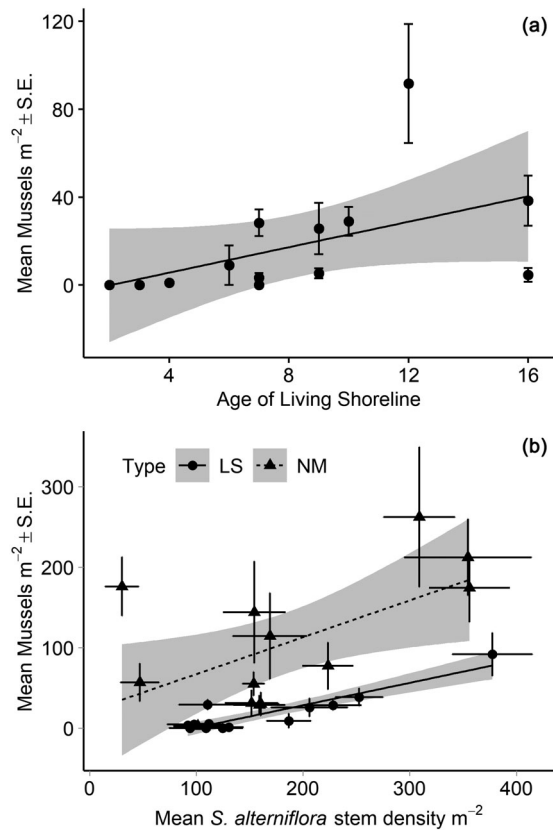


Fig. 4. (a) Mean (\pm SE) ribbed mussel abundance in Chesapeake Bay living shoreline marshes ($n = 13$) aged between 2 and 16 yr that were surveyed during 2018. There was a significant ($P < 0.001$) relationship between mussel density and living shoreline age, suggesting that marsh maturation may lead to more abundant mussels. (b) Ribbed mussel abundance was positively related to cordgrass density, irrespective of age of living shoreline marsh (solid line, living shorelines [LS]; dotted line, natural fringing marshes [NM]). Because cordgrass density was not positively related to marsh age, the observed increase in mussel abundance with marsh age is likely reflective of increases in sediment organic matter that may help alleviate desiccation stress and additional opportunities for annual recruitment in older marshes. Even with increases in mussels with marsh age or cordgrass density, ribbed mussel abundance was significantly lower in living shoreline marshes compared with reference marshes.

on real and perceived need for wave reduction (Fig. 1b). Hindrance of larval mussel access to the marsh may be through several possible

mechanisms, including changing flow patterns near the marsh, the permeability of the structure, or minimizing/obscuring mussel settling cues. For example, sills increase energy regimes on their channel-ward edge and decrease energy regimes on their landward edge, enhancing suspension or deposition, respectively (Airoldi et al. 2005). Even though adult mussels were absent within some living shoreline marshes, juvenile mussels settled on collection pads within all of the living shoreline marshes sampled, indicating that marsh access was possible at these sites. We did not assess the relative levels of recruitment at living shoreline and natural fringing marshes, so further study is needed to more fully quantify larval access, recruitment, and survival. In our study, sill heights were relatively low, cresting near high water levels which would allow for wave overtopping. Sill heights ranged from 0 to 23.3 cm above mean high water (MHW), with mean heights of 5.6 cm above MHW and several sills built to the height of MHW. Although the tallest sill was one of the three sites without adult mussels in the marsh, the other two sites without adult mussels had low sills that did not extend above MHW. Generally, this indicates that sills designed to be at or slightly above MHW are allowing some level of larval mussel access.

Sediment quality

When settling within marshes, ribbed mussels may initially rely on benthic algae for their diet because during early juvenile stages gill filaments are few in number and pedal feeding (using foot cilia to collect particles from the sediment) may dominate or supplement feeding. While we were unable to find reports of ribbed mussels engaging in this behavior, pedal feeding in juvenile freshwater bivalves and other mussel species has been well documented (Vaughn and Hakenkamp 2001) and has been posited to be a primitive trait in all bivalves (Reid et al. 1992). In other mussel species, once gill structures are fully developed, filter feeding becomes most efficient and the transition from pedal feeding to filter feeding occurs (Schartum et al. 2017). Living shorelines are constructed with clean, coarse sand fill; therefore, sediment quality (e.g., organic content and benthic algae) may vary from natural marshes for some time, possibly reducing pedal feeding opportunities by juvenile

mussels (Bilkovic and Mitchell 2017). Benthic algal abundance (micro- and macroalgae) has been shown to be lower in living shorelines, in comparison with reference marshes, but the difference was largely due to reduced macroalgae abundance (O'Connor et al. 2011). We found similar concentrations of chlorophyll *a* (microalgae) in sediments of living shoreline marshes and reference fringing marshes. More research is needed in this area, particularly on the composition of the benthic algae and identification of preferred diet items for young mussels. Another potential sediment quality issue is that soil moisture retention of the sand fill used to create the marsh is lower than in the organic-rich natural marsh sediments. Early mussel recruits are extremely sensitive to desiccation (Seed 1969, Jenewein and Gosselin 2013), and sand fill may dry out the surface layers recruits would inhabit. In this study, living shoreline marsh sediments were coarser, with lower moisture and organic content than reference marshes, which may contribute to larval desiccation. In support, as organic matter content increased in relation to marsh age, mussel density also increased.

Availability of high-quality refuge habitat

Ribbed mussels have a mutualistic relationship with cordgrass (Angelini et al. 2016, Bilkovic et al. 2017b) and higher densities of this marsh plant are correlated with mussel density (Bertness 1984, Honig et al. 2015, Isdell et al. 2018). We also observed this pattern for both living shorelines and paired reference marshes when mussels were present at our sites. Angelini et al. (2015) suggested that dense cordgrass beds may serve as a refuge for ribbed mussels by providing shade to prevent desiccation, as well as attachment surfaces to help secure animals in place and reduce predation risk. Cordgrass density within a created marsh can reach densities of reference marshes within a few years following construction (e.g., Currin et al. 2008), but in some sites densities may remain lower for more than 10 yr (Bilkovic and Mitchell 2017). Because marsh plants are planted on grids, usually with 0.3 m spacing, it can take several years for the marsh to expand into unplanted areas. Marshes planted in a clumped manner (i.e., several plugs planted together) may facilitate the expansion of the marsh and

enhance productivity (Gleason et al. 1979, Silliman et al. 2015). Living shoreline marshes with low cordgrass density may have limited high-quality refuge area for juvenile mussels, contributing to the absence or low abundance of mussels observed. This hypothesis is supported by the positive relationship we observed between cordgrass and mussel density within living shorelines. However, at our study sites, where planting occurred on grids, cordgrass density was not correlated with marsh age, so it cannot be assumed that as a marsh matures, plants will become denser and thereby provide more suitable habitat for ribbed mussels. In addition, juvenile ribbed mussels appear to preferentially select conspecifics (adult mussels) to cluster within marshes (Nielsen and Franz 1995). Young ribbed mussels (<10 mm) can be mobile and may continue to search out preferential marsh microhabitats following initial settlement (Bertness and Grosholz 1985); therefore, the absence/low abundance of conspecifics in many of the living shoreline marshes may be resulting in limited juvenile settlement and/or survival. The lack of adult mussels may necessitate human intervention before populations in living shorelines can be sustained by wild recruitment alone.

Inundation period is linked to both feeding opportunities and predation/desiccation risks and therefore can be a controlling factor in mussel distribution across a marsh surface. In this study, all of the living shorelines had inundation periods similar to or greater than the paired natural marshes, suggesting that these living shoreline marshes reflected natural inundation periods and inundation was not limiting low marsh mussel establishment. To minimize these effects, sills should be properly sized for the wave energy regime and provide tidal access through gaps in the stone, lowered sections of the sill, and/or different sized stone for interstitial access through the sill (Bilkovic and Mitchell 2017). In low energy settings, oyster reef structures may be sufficient to reduce wave energy while maintaining tidal access for young mussels (Bilkovic and Mitchell 2017, Morris et al. 2019). Additional data are needed on access limitations for a range of sill sizes and configurations to help refine design recommendations. Encouragingly, a new US Army Corps of Engineers nationwide permit

for living shorelines issued in 2017 (NWP 54), as well as many state and regional permits, require dropdowns or tidal access points at designated intervals (e.g., every 25 m) and maximum heights for sills of 30 cm above MHW that may help to address this concern.

Biological considerations

The absence of adult ribbed mussel conspecifics in some living shoreline marshes may be restricting larval attraction and settlement. To increase recruitment, mussels could be introduced during or after living shoreline construction. For example, live mussels could be allowed to attach to cordgrass plugs from the nursery prior to planting. Constructing the marsh with a seed population of mussels and in a manner that promotes cordgrass density may help accelerate wild mussel recruitment. Recent efforts to incorporate ribbed mussels into marsh restoration projects in Delaware Bay relied on the presence of mussels in the marsh being enhanced or the use of salvaged marsh plants/mussels from adjacent marshes to encourage mussel recruitment (Moody et al. 2016), but technical difficulties in producing reliable seed sources are hampering wide-spread restoration efforts (Kreeger et al. 2018). Additional research is needed to determine the most effective approach to introducing mussels to living shoreline marshes, especially in conjunction with aggregate cordgrass plantings.

CONCLUSIONS

In summary, along the chronosequence of living shoreline marshes (ages 2–16 yr), cordgrass density, on average, was equivalent to reference marsh cordgrass density with no apparent increase with marsh age, whereas ribbed mussel density and sediment organic matter were not yet equivalent, but increased with living shoreline marsh age. Time to reach functional equivalency for sediment organic matter and mussels exceeds 16 yr. Assuming a post-installation, linear increase in the low marsh surface layer OM (upper 5 cm), living shorelines will approximate the mean OM of natural marshes (6.74%) in about 31 yr. Following marsh sediment maturation, those marshes with dense cordgrass may result in improved mussel recruitment success. In the interim, if an immediate restoration goal is

to enhance ecosystem services provided by ribbed mussels (e.g., water filtration), living shoreline design modifications may be necessary.

By restoring living shoreline marshes for self-sustaining ribbed mussel populations, several valued benefits can be derived, including water clarity improvement and nutrient reduction. Moreover, mussels enhance marsh resilience by capturing sediment and promoting accretion, particularly important in areas experiencing high rates of sea level rise and/or with barriers to landward marsh migration. Furthermore, in the southeastern USA, through their mutualistic relationship with cordgrass, ribbed mussels may alleviate stress (high soil salinity, soil acidification) for cordgrass by enhancing water storage and nutrient availability (Angelini et al. 2016, Derksen-Hooijberg et al. 2019). As the climate continues to warm, extreme events such as droughts are expected to increase in severity and frequency (Hansen et al. 2012) and ribbed mussels may contribute to the resistance and/or recovery of salt marshes to droughts throughout their range. In this manner, mussels have the potential to contribute to both near- and long-term resilience of coastal habitats. The discussed possible adjustments to design and implementation practices to encourage mussel recruitment should be considered and further studied in the Chesapeake Bay region and throughout the Atlantic and Gulf Coasts where similar living shoreline projects are being implemented and ribbed mussels occur.

Climate and human pressures are likely to lead to a redistribution of salt marsh habitat in estuaries surrounded by densely populated watersheds like Chesapeake Bay. In areas with high rates of sea level rise, the persistence of a given marsh will be largely dependent on marsh migration potential (Mitchell et al. 2017). In Chesapeake Bay, ribbed mussel habitat is expected to decrease in total area, with expansion in rural landscapes that have the capacity for marsh migration (less shoreline armoring and more pervious land cover), and loss in urbanized landscapes (more armoring and impervious surfaces) where we expect significant coastal squeeze (Isdell 2018). Living shoreline marshes with fronting sills, which enhance sediment capture rates (Currin et al. 2008) and dissipate wave energy protecting the sediment

below the root depth, may be able to persist under sea level rise conditions longer than natural marshes (Mitchell and Bilkovic 2019). The design practices recommended here to encourage ribbed mussel recruitment will also likely contribute to the resilience of these projects (e.g., dense plantings). In areas with expected marsh and mussel loss, living shoreline marshes may subsidize mussel populations, if adjustments to implementation practices succeed in enhancing mussel recruitment to these created habitats.

Finally, to maximize the value of living shorelines, a cross-disciplinary, adaptive-management approach to restoration should be adopted. The tangible goal to enhance bivalves in living shorelines can serve as an opportunity to engage diverse shoreline restoration partners including restoration practitioners, ecologists, engineers, landscape designers, managers, and local communities in the experimental evaluation of various designs and practices toward enhanced ecological performance of created marshes.

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LITERATURE CITED

Airoldi, L., M. Abbiati, M. W. Beck, S. J. Hawkins, P. R. Jonsson, D. Martin, P. S. Moschella, A. Sundelöf, and R. C. Thompson, and P. Åberg. 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coastal Engineering* 52:1073–1087.

- Angelini, C., J. N. Griffin, J. van de Koppel, L. P. Lamers, A. J. Smolders, M. Derksen-Hooijberg, T. van der Heide, and B. R. Silliman. 2016. A keystone mutualism underpins resilience of a coastal ecosystem to drought. *Nature Communications* 7:1–8.
- Angelini, C., T. van der Heide, J. N. Griffin, J. P. Morton, M. Derksen-Hooijberg, L. P. Lamers, A. J. Smolders, and B. R. Silliman. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society B: Biological Sciences* 282:20150421.
- Arar, E. J., and G. B. Collins. 1997. Method 445.0: in vitro determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. United States Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory, Washington, D.C., USA.
- Arkema, K. K., G. Guannel, G. Verutes, S. A. Wood, A. Guerry, M. Ruckelshaus, P. Kareiva, M. Lacayo, and J. M. Silver. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change* 3:913–918.
- Arribas, L. P., M. Bagur, J. L. Gutiérrez, and M. G. Palomo. 2015. Matching spatial scales of variation in mussel recruitment and adult densities across southwestern Atlantic rocky shores. *Journal of Sea Research* 95:16–21.
- Baker, P., and R. Mann. 1997. The postlarval phase of bivalve mollusks: a review of functional ecology and new records of postlarval drifting of Chesapeake Bay bivalves. *Bulletin of Marine Science* 61:409–430.
- Beck, A. J., R. M. Chambers, M. M. Mitchell, and D. M. Bilkovic. 2017. Evaluation of living shoreline marshes as a tool for reducing nitrogen pollution in coastal systems. Pages 271–289 in D. M. Bilkovic, M. Mitchell, M. La Peyre, and J. Toft, editors. *Living shorelines: The science and management of nature-based coastal protection*. CRC Press, Taylor & Francis Group, Boca Raton, Florida, USA.
- Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* 65:1794–1807.
- Bertness, M. D., C. P. Brisson, and S. M. Crotty. 2015. Indirect human impacts turn off reciprocal feedbacks and decrease ecosystem resilience. *Oecologia* 178:231–237.
- Bertness, M. D., and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67:192–204.
- Bilkovic, D. M., and M. M. Mitchell. 2013. Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages. *Ecological Engineering* 61:469–481.
- Bilkovic, D. M., and M. M. Mitchell. 2017. Designing living shoreline salt marsh ecosystems to promote coastal resilience. Pages 293–316 in D. M. Bilkovic, M. Mitchell, M. La Peyre, and J. Toft, editors. *Living shorelines: The science and management of nature-based coastal protection*. CRC Press, Taylor & Francis Group, Boca Raton, Florida, USA.
- Bilkovic, D. M., M. M. Mitchell, J. Toft, and M. La Peyre. 2017a. A Primer to Living Shorelines. Pages 3–9 in D. M. Bilkovic, M. Mitchell, M. La Peyre, and J. Toft, editors. *Living shorelines: The science and management of nature-based coastal protection*. CRC Press, Taylor & Francis Group, Boca Raton, Florida, USA.
- Bilkovic, D. M., M. M. Mitchell, R. E. Isdell, M. Schliep, and A. R. Smyth. 2017b. Mutualism between ribbed mussels and cordgrass enhances salt marsh nitrogen removal. *Ecosphere* 8:e01795.
- Bilkovic, D. M., M. M. Mitchell, P. Mason, and K. Duhring. 2016. The role of living shorelines as estuarine habitat conservation strategies. *Coastal Management* 44:161–174.
- CCRM [Center for Coastal Resources Management]. 2017. Shoreline permit database. Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA.
- Chambers, R. M., A. L. Gorsky, R. E. Isdell, M. M. Mitchell, and D. M. Bilkovic. 2020. Comparison of nutrient accrual in constructed living shoreline and natural fringing marshes. *Ocean & Coastal Management* 199:105401.
- Chesson, P. 1998. Recruitment limitation: a theoretical perspective. *Australian Journal of Ecology* 23:234–240.
- Craft, C., P. Megonigal, S. Broome, J. Stevenson, R. Freese, J. Cornell, L. Zheng, and J. Sacco. 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecological Applications* 13:1417–1432.
- Currin, C. A., P. C. Delano, and L. M. Valdes-Weaver. 2008. Utilization of a citizen monitoring protocol to assess the structure and function of natural and stabilized fringing salt marshes in North Carolina. *Wetlands Ecology Management* 16:97–118.
- Derksen-Hooijberg, M., C. Angelini, J. R. Hoogveld, L. P. Lamers, A. Borst, A. Smolders, S. F. Harpenslager, L. L. Govers, and T. van der Heide. 2019. Repetitive desiccation events weaken a salt marsh mutualism. *Journal of Ecology* 107:2415–2426.
- Folk, R. L. 1980. Petrology of sedimentary rocks. Hemphill, Austin, Texas, USA.

- Galimany, E., G. H. Wikfors, M. S. Dixon, C. R. Newell, S. L. Meseck, D. Henning, Y. Li, and J. M. Rose. 2017. Cultivation of the Ribbed Mussel (*Geukensia demissa*) for Nutrient Bioextraction in an Urban Estuary. *Environmental Science & Technology* 51:13311–13318.
- Gittman, R. K., C. H. Peterson, C. A. Currin, J. F. Fodrie, M. F. Piehler, and J. F. Bruno. 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications* 26:249–263.
- Gittman, R. K., A. M. Popowich, J. F. Bruno, and C. H. Peterson. 2014. Marshes with and without sills protect estuarine shorelines from erosion better than bulkheads during a Category 1 hurricane. *Ocean & Coastal Management* 102:94–102.
- Glason, M. L., D. A. Elmer, N. C. Pien, and J. S. Fisher. 1979. Effects of stem density upon sediment retention by salt marsh cord grass, *Spartina alterniflora* Loisel. *Estuaries* 2:271–273.
- Hansen, J., M. Sato, and R. Ruedy. 2012. Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America* 109:E2415–E2423.
- Honig, A., J. Supan, and M. L. Peyre. 2015. Population ecology of the gulf ribbed mussel across a salinity gradient: recruitment, growth and density. *Ecosphere* 6:1–3.
- Isdell, R. E. 2018. Shifting patterns of ribbed mussel distribution and ecosystem services in response to sea level rise. Dissertation. William & Mary, Williamsburg, Virginia, USA.
- Isdell, R. E., D. M. Bilkovic, and C. Hershner. 2018. Shorescape-level factors drive distribution and condition of a salt marsh facilitator (*Geukensia demissa*). *Ecosphere* 9:e02449.
- Jenewein, B. T., and L. A. Gosselin. 2013. Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: effects of desiccation and heat on juvenile mortality. *Marine Ecology Progress Series* 481:147–159.
- Jordan, T. E., and I. Valiela. 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnology and Oceanography* 27:75–90.
- Jost, J., and B. Helmuth. 2007. Morphological and ecological determinants of body temperature of *Geukensia demissa*, the Atlantic ribbed mussel, and their effects on mussel mortality. *Biological Bulletin* 213:141–151.
- Kreeger, D. A., C. M. Gatenby, and P. W. Bergstrom. 2018. Restoration potential of several native species of bivalve molluscs for water quality improvement in Mid-Atlantic watersheds. *Journal of Shellfish Research* 37:1121–1158.
- Kreeger, D. A., and R. I. E. Newell. 2001. Seasonal utilization of different seston carbon sources by the ribbed mussel, *Geukensia demissa* (Dillwyn) in a mid-Atlantic salt marsh. *Journal of Experimental Marine Biology and Ecology* 260:71–91.
- Leonard, L. A., and A. L. Croft. 2006. The effect of standing biomass on flow velocity and turbulence in *Spartina alterniflora* canopies. *Estuarine, Coastal and Shelf Science* 69:325–336.
- Loosanoff, V. L., and H. C. Davis. 1963. Rearing of bivalve mollusks. *Advances in Marine Biology* 1: 1–136.
- Mitchell, M., and D. M. Bilkovic. 2019. Embracing dynamic design for climate-resilient living shorelines. *Journal of Applied Ecology* 56:1099–1105.
- Mitchell, M., J. Herman, D. M. Bilkovic, and C. Hershner. 2017. Marsh persistence under sea-level rise is controlled by multiple, geologically variable stressors. *Ecosystem Health and Sustainability* 3:1379888.
- Moody, J., and D. Kreeger. 2020. Ribbed mussel (*Geukensia demissa*) filtration services are driven by seasonal temperature and site-specific seston variability. *Journal of Experimental Marine Biology and Ecology* 522:151237.
- Moody, J., D. Kreeger, S. Bouboulis, S. Roberts, and A. Padeletti. 2016. Design, implementation, and evaluation of three living shoreline treatments at the DuPont Nature Center, Mispillion River, Milford, DE. Partnership for the Delaware Estuary, Wilmington, Delaware, USA. Report No. 16–12. https://s3.amazonaws.com/delawareestuary/PDE-Report-16-12_Mispillion_FINAL_April2017.pdf
- Morris, R. L., et al. 2019. The application of oyster reefs in shoreline protection: Are we over-engineering for an ecosystem engineer? *Journal of Applied Ecology* 56:1703–1711.
- Narayan, S., M. W. Beck, B. G. Reguero, I. J. Losada, B. Van Wesenbeeck, N. Pontee, N. Sanchirico, J. C. Ingram, G. M. Lange, and K. A. Burks-Copes. 2016. The effectiveness, costs and coastal protection benefits of natural and nature-based defences. *PLOS ONE* 11:e0154735.
- Nielsen, K. J., and D. R. Franz. 1995. The influence of adult conspecifics and shore level on recruitment of the ribbed mussel *Geukensia demissa* (Dillwyn). *Journal of Experimental Marine Biology and Ecology* 188:89–99.
- O'Connor, M. I., C. R. Violin, A. Anton, L. M. Ladwig, and M. F. Piehler. 2011. Salt marsh stabilization affects algal primary producers at the marsh edge. *Wetlands Ecology and Management* 19: 131–140.

- O'Donnell, J. E. D. 2016. Living Shorelines: a review of literature relevant to New England Coasts. *Journal of Coastal Research* 33:435–451.
- Reid, R. G., R. F. McMahon, D. Ó. Foighil, and R. Finigan. 1992. Anterior inhalant currents and pedal feeding in bivalves. *Veliger* 35:93–104.
- Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 71:319–392.
- Schartum, E., S. Mortensen, K. Pittman, and P. J. Jakobsen. 2017. From pedal to filter feeding: ctenidial organogenesis and implications for feeding in the postlarval freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758). *Journal of Molluscan Studies* 83:36–42.
- Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamelli-branchiata) on exposed rocky shores. *Oecologia* 3:277–316.
- Shepard, C. C., C. M. Crain, and M. W. Beck. 2011. The protective role of coastal marshes: a systematic review and meta-analysis. *PLOS ONE* 6: e27374.
- Silliman, B. R., E. Schrack, Q. He, R. Cope, A. Santoni, T. van der Heide, R. Jacobi, M. Jacobi, and J. Van De Koppel. 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proceedings of the National Academy of Sciences of the United States of America* 112:14295–14300.
- Smith, C. S., R. K. Gittman, I. P. Neylan, S. B. Scyphers, J. P. Morton, F. J. Fodrie, J. H. Grabowski, and C. H. Peterson. 2017. Hurricane damage along natural and hardened estuarine shorelines: using homeowner experiences to promote nature-based coastal protection. *Marine Policy* 81:350–358.
- Sutton-Grier, A. E., K. Wowk, and H. Bamford. 2015. Future of our coasts: the potential for natural and hybrid infrastructure to enhance the resilience of our coastal communities, economies and ecosystems. *Environmental Science & Policy* 51:137–148.
- Turley, B., K. Reece, J. Shen, J. H. Lee, X. Guo, and J. McDowell. 2019. Multiple drivers of interannual oyster settlement and recruitment in the lower Chesapeake Bay. *Conservation Genetics* 20:1057–1071.
- Vaughn, C. C., and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46:1431–1446.
- Virgin, S. D., K. A. Sorochan, A. Metaxas, and M. A. Barbeau. 2019. Effect of temperature on the larval biology of ribbed mussels (*Geukensia demissa*) and insights on their northern range limit. *Journal of Experimental Marine Biology and Ecology* 512:31–41.
- Wainger, L. A. 2012. Opportunities for reducing total maximum daily load (TMDL) compliance costs: lessons from the Chesapeake Bay. *Environmental Science & Technology* 46:9256–9265.
- Ward, J. E., and S. E. Shumway. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 300:83–130.

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