

## Ecological equivalency of living shorelines and natural marshes for fish and crustacean communities

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### ABSTRACT

Salt marshes provide valued services to coastal communities including nutrient cycling, erosion control, habitat provision for crustaceans and fish (including juvenile and forage fish), and energy transfer from the detrital based food web to the greater estuarine system. Living shorelines are erosion control structures that recreate natural shorelines, such as fringing marshes, while providing other beneficial ecosystem services. Living shorelines are expected to provide fish and crustacean (nekton) habitat, but few comprehensive studies have evaluated nekton habitat use across a range of living shoreline settings and ages. We sampled the intertidal marsh and subtidal shallow water nekton community at 13 paired living shoreline and reference marsh sites, with living shorelines ranging in age from 2 to 16 years from construction. We compared nekton diversity, nekton community abundance, nekton community biomass, forage abundance, and juvenile abundance at reference marshes and living shorelines. Our results indicate that living shorelines are providing suitable marsh habitat for nekton communities, including juveniles and forage base species. The difference in living shoreline construction (rock sill, soil composition) did not appear to diminish habitat quality in the marsh or in nearshore waters, and rock sills may provide enhanced structural shoreline habitat. Living shorelines have the potential to combat marsh habitat loss and provide resilient nekton nursery habitat.

### 1. Introduction

Coastal communities and environments are increasingly threatened by climate change due to loss or hardening of shorelines that results in property damages for coastal residents and reduced habitat availability for aquatic and estuarine species (Gittman et al., 2015; Nicholls et al., 1999). Sea level rise, more frequent storms, and increased erosion have and will continue to reduce societal sustainability and economic stability (Leonardi et al., 2016; Shepard et al., 2011). Coastal development and hard shoreline modifications for erosion control (e.g., bulkhead, riprap revetment) degrade coastal ecosystems and diminish the natural resilience and adaptive capacity of coastal environments (Gittman et al., 2015; Sutton-Grier et al., 2015).

Coastal wetlands, such as salt marshes, are particularly vulnerable to anthropogenic stressors, and their loss results in a corresponding reduction in ecosystem functioning and valued services (Gilby et al.,

2020). Salt marshes benefit society by attenuating waves, reducing erosion, and withstanding sea level rise along populated shorelines (Leonardi et al., 2016; Möller et al., 2014). Salt marshes benefit ecosystems by providing nekton (fish and crustaceans) with food, predation refuge, and nursery habitat (Banikas and Thompson, 2012; Minello et al., 2003; Quan et al., 2007; Sheaves, 2009). Furthermore, salt marshes subsidize the estuarine food web through trophic transfer of the detrital-based food web (Deegan et al., 2002). Along the southeastern Atlantic and Gulf coasts of the United States, most economically valued fish inhabit or use the marshes as juveniles (Mitsch and Gosselink, 2015). Nekton that forage in the marsh can also be prey for commercially and recreationally valued fish species (Deegan et al., 2002; Kneib, 1986; Laffaille et al., 1998). These sociocultural benefits underscore the key role of salt marshes in supporting estuarine ecosystems, societal resilience, and coastal economies.

Natural and nature-based shoreline protection, henceforth living

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shorelines, incorporate features of natural habitats (e.g., fringing salt marshes) to protect coastal property while providing other valuable benefits to society and ecosystems (Smith et al., 2020). Living shorelines are being implemented to reduce coastal erosion using restored or created habitats that exhibit natural capacity to adapt to changing environments, such as sea level rise and climate change (Bilkovic et al., 2016). Designed to emulate nearby natural habitats and processes, living shorelines are expected to provide similar ecosystem services as their natural counterparts, such as water filtration, wave attenuation, and nutrient cycling (Currin et al., 2010). In the Chesapeake Bay, living shorelines often include fringing salt marshes and additional structural materials in front of the marsh, such as a rock sill or oyster reef, which enhance shoreline protection in higher energy environments. These additional structural features potentially diversify the habitat complexity and may increase the ability of vegetated shorelines to keep pace with sea level rise (Smith et al., 2020; Waltham et al., 2021). Living shorelines tend to resist and recover from hurricanes and storm surges better than shoreline armoring (Gittman et al., 2014; Smith et al., 2018), demonstrating their expected resiliency under future climate regimes.

The structural similarity of living shoreline marshes to natural marshes often is assumed to equate to similar ecological functions, such as nursery habitat and foraging opportunities for fish and crustaceans. Because of variable construction practices and the installation of additional structures, living shoreline marshes may create habitats that differ from natural marshes. In higher wave energy settings, for example, living shorelines may require additional engineered wave-break features for enhanced marsh stability. In these hybrid designs, a sill structure often is placed seaward and parallel to the marsh and may be composed of granite rocks (Bilkovic and Mitchell, 2017). In the mid-Atlantic region, the area behind a sill can be filled with clean sand fill to replicate appropriate tidal elevations and a salt marsh can be created or supplemented with cordgrass (*Spartina alterniflora*) and salt hay (*S. patens*) plantings (Bilkovic and Mitchell, 2017).

Although the practice of using living shorelines has increased over the years (Berman et al., 2018), few studies have comprehensively evaluated how well a living shoreline replicates suitable nekton habitat across multiple environmental settings. Studies in North Carolina, USA, have found that living shorelines that were constructed at least 3 years prior had similar or higher fish abundance and biodiversity than reference marshes (Currin et al., 2008; Gittman et al., 2016). In Maryland, small-bodied fishes, such as mummichog (*Fundulus heteroclitus*), were quick to establish at a newly created living shoreline marsh, but this study was not able to fully evaluate juvenile habitat use as the research was completed after living shoreline creation which occurred after summer recruitment (Davis et al., 2008). In Delaware, Balouskus and Targett (2016) showed that nekton habitat at a living shoreline was more similar to a nearby natural marsh than it was to a nearby riprap revetment. To more fully evaluate the ecological role and nekton habitat suitability of living shorelines within an estuary, there is a need to assess multiple living shorelines in a range of settings and with varying ages since construction.

Living shorelines are expected to increase marsh habitat connectivity along shorescapes (i.e., the tidal shoreline area that includes the riparian, intertidal, and nearshore zones) that are highly developed and habitats that are often fragmented (Waltham et al., 2021). Human-induced marsh fragmentation occurs either directly via replacement of marshes with hardened structures or indirectly where human features influence ecological processes beyond their physical location (Forman and Deblinger, 2000). Habitats in connected shorescapes may be subsidized by surrounding habitats, while those in highly fragmented shorescapes may suffer the effects of isolation. Habitat fragmentation has been linked with shifts in biodiversity, loss of habitat-specific sensitive or functionally important species, and isolation of populations when connectivity is diminished (Fahrig, 2003; Kareiva and Wennergren, 1995; Thrush et al., 2008), but estuarine systems have been far less studied than terrestrial systems even though estuaries and coasts have

experienced substantial habitat loss and fragmentation (e.g., Lotze, 2006).

For the current study, we assessed the extent to which living shoreline marshes reach functional equivalency with fringing marshes to support habitat provisioning. We evaluated nekton community assemblages and fish condition across a range of living shoreline ages and environmental settings. Our two objectives were to 1) examine nekton community structure along a chronosequence of living shorelines in relation to natural fringing marshes (henceforth reference marshes), and 2) relate environmental and shoreline characteristics to the juvenile nekton community, forage base community, and forage base fish condition. Because living shoreline construction practices alter shoreline habitat, we hypothesized that nekton community assemblages and the feeding conditions of older living shorelines would be more similar to reference marshes than younger living shorelines. We further hypothesized that living shoreline and reference marshes farther away from other marshes (e.g., surrounded by more armored shorelines) would exhibit lower nekton habitat use.

## 2. Methods

### 2.1. Field sites

Field sites consisted of 13 pairs of living shorelines and reference marshes at shoreline properties throughout southern Chesapeake Bay (Fig. 1). Living shoreline sites were selected from an initial candidate pool of more than 100 living shorelines extracted from the Virginia Shoreline Permit Database (CCRM, 2017). To minimize variation due to different living shoreline designs, all candidate living shorelines had a rock sill, clean sand fill used to create the correct tidal elevations, planted marsh grasses, and were constructed at least 2 years prior to the first sampling in 2018 to allow time for plant establishment. Final living shoreline sites were then selected through stratified random sampling to include sites categorized as having low, moderate, or high marsh connectivity, with 3, 5, and 5 sites, in each respective category. Marsh connectivity within the shorescape was determined based on the closeness to surrounding marshes and breaks in marsh connectivity due to shoreline armoring (Chambers et al., 2021). For each living shoreline, a nearby, natural fringing marsh (at least 30 linear m of marsh edge) was selected as a reference marsh based on similarities in ecological setting (fetch, land use).

### 2.2. Site sampling: marsh characteristics and site setting

Marsh characteristics (low marsh area, inundation duration, cordgrass density, cordgrass height) were assessed per site. We determined the low marsh area (i.e., the area dominated by cordgrass) by walking the low marsh perimeter and marking the boundary with a handheld Trimble Geo 7×. The boundary was converted to an area in ArcGIS Pro. In the Chesapeake Bay, the upper extent of the low marsh is typically mean high water, therefore, the high marsh is only periodically inundated, limiting its utility as nekton habitat. For this reason, we limited the spatial delineation of nekton usage to the vegetated low marsh. For each site, we determined the inundation duration by interpolating the NOAA tidal predictions for each site using marsh elevation data collected via a stadia rod and a handheld Trimble Geo 7× (Bilkovic et al., 2021). Inundation duration reflects the temporal extent that nekton would have access to the marsh, measured in hours of marsh inundation per month, and is an indication of living shoreline design due to the created elevations from the sand fill. To determine smooth cordgrass density and height for each site, we conducted six transects perpendicular to the shoreline, spaced at least 5 m apart. We placed 0.25 m<sup>2</sup> quadrats at the marsh (water) edge and 1 m inland, resulting in 12 samples per site. For each quadrat, we counted the number of smooth cordgrass stems and measured the visual average height of the stems.

Site setting characteristics (marsh distance, shoreline armoring, Bay

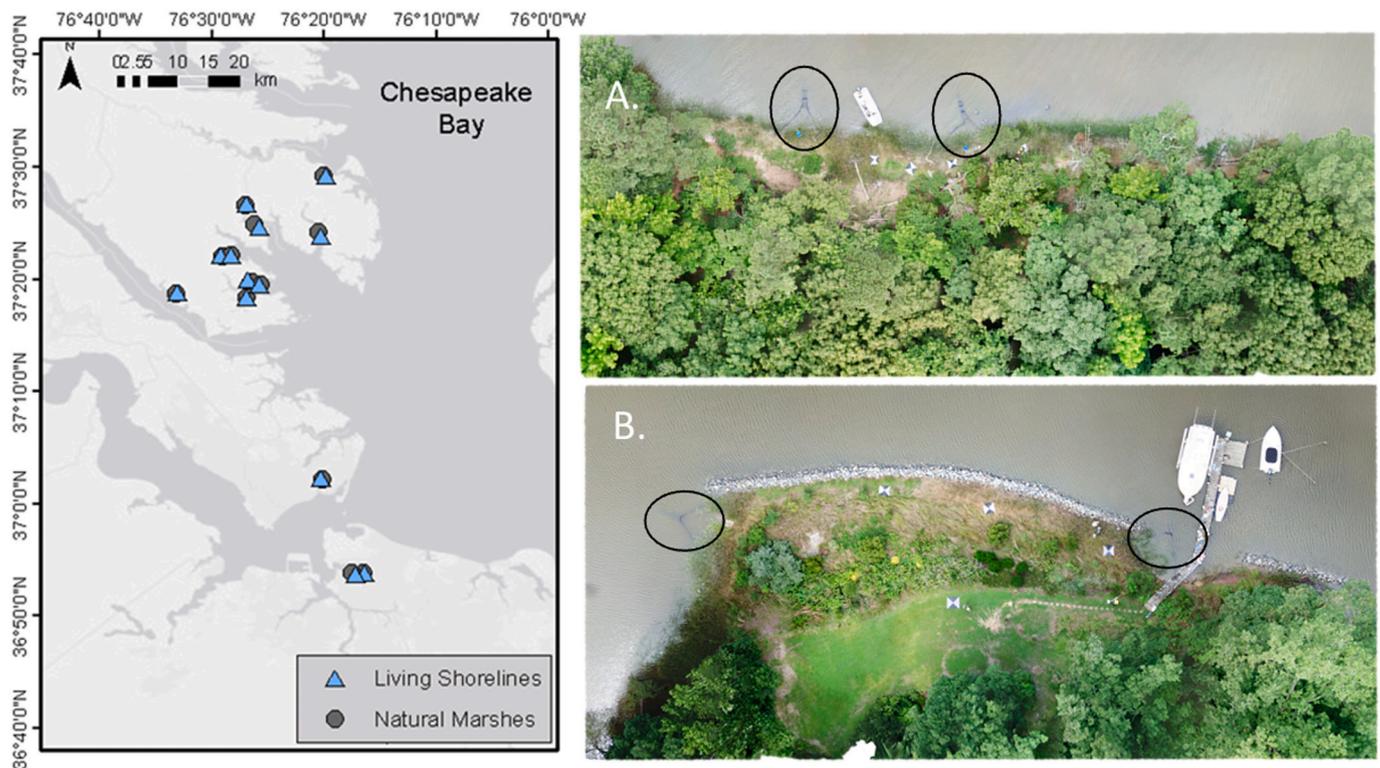


Fig. 1. Field site map and images.

Living shoreline and reference (natural) marsh pairs were sampled throughout the lower Chesapeake Bay, USA. Images of a natural marsh (A) and living shoreline (B) pair during sampling. The two fyke nets for each site are visible in the images, indicated by the black circles.

mouth distance) were assessed per site. Marsh distance was calculated as the mean distance to natural marshes along a 1000 m radius, centered on the site. This marsh distance measure reflects the proximity of surrounding marsh habitat which may influence nekton movement along the shorescape. The measure accounts for marsh connections within and between marsh patches and was used as a relative metric to compare marsh connectivity across sites. Lower marsh distance values indicate there were marshes nearby, and nekton would travel a shorter distance to get to marsh habitat (i.e., higher marsh connectivity). Shoreline armoring is the percent of armoring within a 1000 m radius, centered on the site. Marsh distance was highly correlated with shoreline armoring, such that marshes with high distances to nearby marsh habitat also had high shoreline armoring percentages (Pearson correlation, 0.77), and marsh distance was used for additional analysis. The Bay mouth distance is the shortest distance by water to Chesapeake Bay mouth for each site, which reflects the extent that juvenile or transient species would need to travel from the Atlantic Ocean as a larval source or as part of migration patterns.

### 2.3. Nekton sampling

To assess habitat use, we sampled the nekton community in the intertidal marsh and adjacent subtidal shallow waters during summer (June–August) in 2018 and 2019. At each site, two fyke nets were set at high tide at the marsh edge and retrieved at low tide when the marsh had drained. Fyke nets were placed at the sill gaps or ends of the living shoreline sites and randomly along the edge of the reference marsh sites. To standardize sampling effort, fyke net openings were set at the same distance from marsh edge (~1 m, depending on sill location relative to the marsh edge). The fyke nets consisted of a  $0.9 \times 0.9 \times 3.0$  m compartmentalized, 3.175-mm-mesh bag with  $0.9 \times 5.2$  m wings that stretched out from the bag (set for a total mouth width of 8 m) into the marsh and staked to block a section of low marsh (i.e., wings extend to

high marsh). Fyke nets fished for  $4 \text{ h} \pm 40 \text{ min}$  (SD) and were retrieved at low tide. Ten minnow traps (3 mm mesh size) were set at high tide in cordgrass-dominated low marsh, with five traps near the waterward marsh edge and 5 traps near the cordgrass – salt hay transition zone. Upper traps fished for  $2 \text{ h } 4 \text{ min} \pm 44 \text{ min}$  (SD) and lower traps fished for  $3 \text{ h } 7 \text{ min} \pm 58 \text{ min}$  and were retrieved at mid to low tide. Three seines (7.6 m wide  $\times$  1.8 m tall,  $1.8 \text{ m} \times 1.8 \text{ m} \times 1.2 \text{ m}$  bag, 3.175-mm-mesh,) were pulled at mid-tide, from 15 m offshore towards the marsh edge at reference marshes or the rock sill at living shorelines, with 10-min waiting periods between seines. Physicochemical point measures were recorded at the time of sampling for each site using a handheld YSI® EXO™2. Paired sites were concurrently sampled to reduce temporal variation.

We identified nekton to species, except silverside (*Menidia* spp), anchovy (*Anchoa* spp) and shrimp (*Palaemonetes* spp), which were identified to their respective genus. For each fyke, seine, and minnow trap replicate, we measured each finfish (total length, TL, cm) and we recorded the total weight (g) by species. For abundant species, we measured (TL, cm) a subsample of 25 fish and recorded the total weight (g) by species, by replicate. For blue crabs (*Callinectes sapidus*), we recorded the length (cm; carapace width, CW), weight (g), sex, and sexual maturity (juvenile, adult) of all individuals. For shrimp, we counted all individuals and determined a total weight (g) per sample replicate. We determined species comprising the forage base (Appendix: Table S1), defined broadly as fish and crustacean species that are common along estuarine shorelines and regularly consumed by piscivorous fish (Ihde et al., 2015). We documented which nekton were young-of-year, henceforth juveniles, based on established literature values (Appendix: Table S1). We used TL literature values to correspond with our field measurements when available and fork length and standard length if TL was not reported. Standard length and fork length are shorter measurements than total length, which resulted in a more conservative assessment of juvenile abundance for nine species. If multiple TL

measurements were reported in the literature for summer months, we used the August measurement, which would result in some fish species captured earlier in the summer to be classified as juveniles when they might have been young adults.

To assess the quality of feeding conditions for representative shoreline-associated and marsh-dependent species, the length and individual mass (g) of a subset of adult Atlantic silverside (here, identified to species, *Menidia menidia*, >5 cm TL) and adult mummichog (>4 cm TL) were used to calculate fish condition at each site. Up to 15 Atlantic silverside were collected using the aforementioned seines and 3 additional seine pulls if 15 adults were not captured. If adults were not present in any seines, we measured the lengths and weights of juvenile Atlantic silverside. Up to 30 mummichog were collected using eight additional minnow traps (6 mm mesh size), placed haphazardly in the lower marsh, and at least 1 m away from other traps. These traps were checked between 20- to 40-min after setting to ensure gut contents would be minimally digested. To assess mummichog gut fullness, a proxy for recent feeding opportunities, mummichog were euthanized with a lethal dose of buffered MS-222 and preserved in 10% buffered formalin. As mummichog lack a true stomach, their intestinal sections I and II (i.e., esophagus through the second bend of the intestines; Babkin and Bowie, 1928) were removed and transferred to 70% ethanol after fixation. Total gut weight (g) was recorded.

#### 2.4. Living shoreline age

To assess if there were any nekton community trends with living shoreline age, we calculated the Pearson correlation coefficient for total nekton abundance, juvenile abundance, forage species abundance, mummichog condition, and silverside condition, with living shoreline age (R Core Team, 2020).

#### 2.5. Nekton community abundance and biomass

We calculated site-specific nekton diversity based on species taxonomic distinctness. Taxonomic distinctness incorporates phylogenetic relationships across species to assess differences due to functional groups rather than species-driven differences (Warwick and Clarke, 2001). Taxonomic distinctness was analyzed using PERMANOVA (Permutational multivariate analysis of variance) models using Type III sum of squares and 9999 permutations. We modeled the functional diversity relative to shoreline type, pair number, sampling year, and all two-way interactions terms (PRIMER-E v7 with PERMANOVA extension, Anderson et al., 2008).

To compare the nekton community, we used a square root transformation to down-weight highly abundant species and ran species-species comparisons at the community level (Bray–Curtis similarity matrices) with PERMANOVA (PRIMER-E v7 with PERMANOVA extension, Anderson et al., 2008). We modeled community composition based on pair number, shoreline type, sampling year, and all two-way interactions. Models were run separately using species abundance and species biomass. We conducted separate analyses for the nekton communities found in nearshore, subtidal shallow waters (seines), intertidal marsh habitat (fyke nets and minnow traps), and at the site-level (all fishing methods combined). For nekton captured in the intertidal marsh habitat, we ran the aforementioned PERMANOVA models on the juvenile fish community and the forage base community using species abundance and species biomass.

For any community differences detected in the PERMANOVAs between shoreline types ( $p < 0.05$ ), we ran a SIMPER analysis (Similarity percentages) to identify which species were driving the differences (PRIMER-E v7 with PERMANOVA extension, Anderson et al., 2008). These identifications were made based on the Diss/SD ratio, which is the average contribution of a species divided by the standard deviation of its contributions. Larger values indicate the species more often contributed to differences detected. Species with a Diss/SD value over 1.1 were

considered to be predominately driving the differences between shoreline types. For these key species, we compared their size distributions at living shorelines and at reference marshes in R statistical software environment (henceforth, R) using Kolmogorov-Smirnov tests (R Core Team, 2020).

#### 2.6. Juvenile and forage species abundance and site factors

We evaluated the extent that site factors (marsh characteristics, site setting) influence the abundance of juveniles and the forage base. We developed separate models for juvenile abundance and forage base abundance based on marsh characteristics (Eq. (1)) and site setting (Eq. (2)). All generalized linear mixed-effects models were conducted using the lme4 package in R 4.0.3 (Bates et al., 2015; R Core Team, 2020).

$$abundance_{i,j} = \beta_1 area_i + \beta_2 inundation_i + \alpha_{0,j} + \epsilon_{i,j} \quad (1)$$

The marsh characteristics model (Eq. (1)) included two fixed effects: 1)  $area_i$  which is the low marsh area for site  $i$ , and 2)  $inundation_i$ , which is the hours of low marsh inundation per month for site  $i$ . Pair number  $j$  was included as a random factor,  $\alpha_{0,j}$ .

$$abundance_{i,j} = \beta_1 marsh\ dist_i + \beta_2 mouth\ dist_i + \alpha_{0,j} + \epsilon_{i,j} \quad (2)$$

The site setting model (Eq. (2)) included two fixed variables: 1)  $marsh\ dist_i$ , which is marsh connectivity measure of the mean distance to surrounding natural marshes along a 1000-m shorescape, centered on site  $i$ , (i.e., a lower marsh distance value indicates higher connectivity to marsh habitat), and 2)  $mouth\ dist_i$ , which is the distance by water from site  $i$  to Chesapeake Bay mouth. Pair number  $j$  was included as a random factor,  $\alpha_{0,j}$ .

For both models, we averaged the site-specific abundances across years because the marsh characteristics and site setting were consistent across years. We modeled juvenile abundance as a negative binomial distribution (which drops the error term) and the forage base abundance as a normal distribution using *glmer* and *lmer* functions, respectively. Bay mouth distance was log-transformed to meet assumptions of normality. To permit comparisons of variable effect sizes (i.e., compare  $\beta$  coefficients), all variables were standardized and centered. Models were compared to each other and to the null model using Akaike information criterion (AIC), which incorporates model goodness of fit and penalties for models with more variables (Aho et al., 2014). We calculated  $\Delta AIC$ , which is the difference of the model AIC compared to the null model AIC, with larger values indicating better model fit.

We used mummichog to evaluate the quality of feeding conditions in intertidal marsh habitat, and Atlantic silverside to compare nearshore subtidal conditions. Mummichog are a marsh-resident species, and are one of the most abundant shoreline species with a highly localized home range and high site fidelity (Currin et al., 2003; Lotrich, 1975). Atlantic silverside prefer nearshore habitat during the growing season and are a highly abundant forage fish (Balouskus and Targett, 2012). Mummichog and Atlantic silverside are common prey items for recreationally and commercially important fishes, such as *Morone saxatilis* (striped bass) and *Pomatomus saltatrix* (bluefish; Balouskus and Targett, 2012; Tupper and Able, 2000).

We calculated mummichog and Atlantic silverside fish condition with Fulton's condition factor,  $K$  (Eq. (3); Blackwell et al., 2000; Bolger and Connolly, 1989).

$$K = (Weight/Length^3) \times 100,000 \quad (3)$$

Under isometric growth, fish weight (*Weight*) is expected to be proportional to fish length cubed ( $Length^3$ ), and thus the ratio of measured weight over expected weight provides an indication of the relative plumpness of the fish.

We modeled how Atlantic silverside and mummichog fish condition related to marsh characteristics, site setting, and shoreline type. The former two models include the same model structure as described above

for abundance (Eqs. (1), (2)). The shoreline type model (Eq. (4)) included shoreline type ( $type_i$ ) and year ( $year_i$ ) as fixed effects for site  $i$  and pair  $j$  was included as a random effect ( $\alpha_{0,j}$ ).

$$Condition_{i,j} = \beta_1 type_i + \beta_2 year_i + \alpha_{0,j} + \epsilon_{i,j} \quad (4)$$

Mummichog condition and Atlantic silverside condition were normally distributed. Mummichog and Atlantic silverside condition linear models were conducted using the lme4 package in R (Bates et al., 2015; R Core Team, 2020), and compared using  $\Delta AIC$ , as described above.

To assess feeding conditions within the marsh, we calculated mummichog gut fullness (GF, Eq (5)). Gut fullness assesses the immediate environmental feeding conditions before sampling, using gut weight (*gut content mass*) normalized to total body weight (*total body mass*) for comparisons among individuals (Hyslop, 1980).

$$GF = \text{gut content mass} / \text{total body mass} \quad (5)$$

We modeled mummichog GF using the same model structures described previously for marsh characteristics, site setting, and shoreline type (Eqs. (1), (2), and (4), respectively), and models were compared based on their  $\Delta AIC$ . Gut fullness was fit using a normal distribution, and models were conducted using the lme4 package in R 4.0.3 (Bates et al., 2015; R Core Team, 2020).

### 3. Results

#### 3.1. Nekton and site sampling

In 2018 and 2019, respectively, we collected: 22,680 and 20,525 fish; 792 and 1262 blue crabs; 3487 and 5545 shrimp; with a total nekton biomass of 65,084 g and 56,087 g. We captured 37 species in 2018 and 36 species in 2019 resulting in 43 different species across both years. In total, 19 species were considered forage species (Appendix: Table S1), and 33 species were comprised of more than 50% juveniles over both years. At each site, we captured 15 adult Atlantic silverside for additional body condition analysis, except at four living shoreline sites and one reference marsh site in 2018 and at two living shoreline sites and four reference marshes in 2019, where Atlantic silverside availability was limited. One reference marsh site in 2019 had no Atlantic silverside, either adults or juveniles. Similarly, at each site we captured 30 adult mummichog for body condition and gut fullness assessments, except for one living shoreline site in 2019, where we were only able to capture 25 adult mummichog.

Marsh characteristics and site setting were similar at living shoreline and reference marsh sites (Appendix: Table S3). All values, below, are reported as means and standard errors. In 2018 and 2019, respectively, the water temperature was  $29.2 \pm 0.3$  °C and  $28.1 \pm 0.5$  °C, salinity was  $15.3 \pm 0.4$  and  $15.9 \pm 0.4$ , and dissolved oxygen was  $7.3 \pm 0.4$  mg/L and  $5.7 \pm 0.2$  mg/L. The average low marsh area was  $215 \pm 34$  m<sup>2</sup>, and inundation duration was  $187 \pm 15$  h per month. From any given point within a 1 km radius of each site, the average distance to nearby marsh habitat was  $13 \pm 2$  m, the distance to the Chesapeake Bay mouth was  $51 \pm 3$  km, and percent natural land cover was  $59 \pm 4\%$ . For living shorelines and natural marshes, respectively, mean cordgrass height was  $83 \pm 6$  cm and  $81 \pm 5$  cm, and mean cordgrass density was  $163 \pm 23$  stems per m<sup>2</sup> and  $182 \pm 28$  stems per m<sup>2</sup>.

#### 3.2. Living shoreline age

We did not find any significant correlations of living shoreline age with any nekton abundance metrics, or fish condition. All Pearson correlation coefficients were within  $\pm 0.05$  of zero, except juvenile abundance which had a correlation coefficient of 0.11 (Table 1).

**Table 1**

Living shoreline age Pearson coefficient correlations.

| Nekton metric        | Correlation |
|----------------------|-------------|
| Nekton Abundance     | -0.05       |
| Juvenile Abundance   | 0.11        |
| Forage Abundance     | -0.03       |
| Mummichog Condition  | 0.04        |
| Silverside Condition | 0.04        |

Correlation with nekton metrics and living shoreline age since construction. Based on the sampling in 2018, living shoreline age ranged from 2 to 16 years, and no nekton metrics were correlated with living shoreline age.

#### 3.3. Habitat suitability: nekton abundance and biomass

Nekton species abundance was similar between living shorelines and reference marshes (PERMANOVA,  $p > 0.05$ , Appendix: Table S4), but biomass differed by shoreline type at the site-level, and in the intertidal marsh habitat (PERMANOVA,  $p < 0.05$ , Table 2). There were no differences detected in community abundance or biomass for the subtidal community or in the intertidal community based on site type (PERMANOVA,  $p > 0.05$ , Appendix: Tables S5, S6). Nekton functional diversity was similar at living shoreline and natural marsh sites (Appendix: Table S7). There were no differences in any results when we considered fish and crustaceans together or separately; therefore, all presented results include the entire nekton community. For all community comparisons, the multivariate dispersions at living shorelines and reference marshes were homogenous (PERMDISP,  $p > 0.05$ ).

Nekton biomass differences in marshes (i.e., fyke nets and minnow traps) were influenced by higher biomass of mummichog, blue crab, striped killifish (*Fundulus majalis*), shrimp, and silverside in living shoreline marshes relative to reference marshes (SIMPER, DISS/SD  $> 1.1$ , Table 2). At the site level (i.e., all fishing gear), differences were influenced by higher biomass of mummichog, blue crab, striped killifish, spot (*Leiostomus xanthurus*), and shrimp at living shorelines, and higher biomass of silverside and anchovy at reference sites than at living shoreline sites (SIMPER, DISS/SD  $> 1.1$ , Appendix: Table S4). In all comparisons, pair number was significantly related to the community composition abundance and biomass (Tables 1, S3, S4, S5, S6).

**Table 2**

Marsh community biomass comparisons in marsh habitat.

|                                     | All Nekton Biomass  | Forage Biomass   | Juvenile Biomass |
|-------------------------------------|---|--|------------------|
| Pair number                         | 0.0001  | 0.0001   | 0.0191           |
| Shoreline Type                      | 0.0233  | 0.0139   | 0.1057           |
| Species contributing to differences | Mummichog*<br>Striped killifish*<br>Blue crab*<br>Shrimp spp.*<br>Silverside*<br>Silver perch<br>Spot | Mummichog*<br>Striped killifish*<br>Blue crab*<br>Shrimp spp.*<br>Silver perch | NS               |
| Year                                | 0.1147  | 0.1127   | 0.1327           |
| Pair x Type                         | 0.0003  | 0.004  | 0.2009           |
| Pair x Year                         | 0.0005  | 0.0007   | 0.1349           |
| Type x Year                         | 0.4141  | 0.3431   | 0.5808           |

Comparisons of biomass for all nekton, forage nekton, and juvenile nekton captured in the intertidal marsh habitat (fyke nets, minnow traps). Table reports p-values, with an  $\alpha$  level of 0.05. If there was a difference detected due to shoreline type, the species that were driving the difference were assessed with a SIMPER analysis. All species were determined to have higher biomass at living shoreline sites. The species dominating the difference (Diss/SD  $> 1.1$ ) are marked with \*.

### 3.4. Habitat suitability: juvenile and forage species patterns

The juvenile nekton marsh community captured on the intertidal marsh habitat was similar at living shorelines and reference marshes, for abundance (PERMANOVA,  $p > 0.05$ , Appendix: Table S5) and biomass (PERMANOVA,  $p > 0.05$ , Table 2). The forage community captured in intertidal marsh habitat had similar abundances across shoreline type (PERMANOVA,  $p > 0.05$ , Appendix: Table S5), but living shorelines had higher biomass, driven by striped killifish, blue crabs, mummichog, silverside, and shrimp (PERMANOVA,  $p < 0.05$ ; SIMPER, DISS/SD  $> 1.1$ ; Table 2).

We compared the size-frequency distributions of the striped killifish, blue crab, mummichog, and silverside that influenced biomass differences between living shoreline and reference marshes. All four species had significantly different distributions (Kolmogorov–Smirnov,  $p < 0.05$ , Fig. 2). Shrimp contributed to biomass differences, but we did not record their lengths, so a size-frequency comparison across habitat types was not possible. Striped killifish were more abundant at living shorelines, and there were higher abundances of smaller ( $< 3$  cm) and larger fish ( $> 7$  cm) than at reference marshes. Mummichog tended to be larger at living shorelines within the same size classes as there is a clear distinction between juvenile and adult size classes, around 5–6 cm. Silverside were often smaller at living shorelines and were larger at reference marshes. Blue crabs in reference marshes and living shorelines had similar size distribution patterns, although significant differences were detected. Unlike the other size-frequency species comparisons, these detected differences in blue crab sizes do not present a clear pattern, and differences detected are likely due to the natural variation present in a large sample size ( $n = 1863$ ).

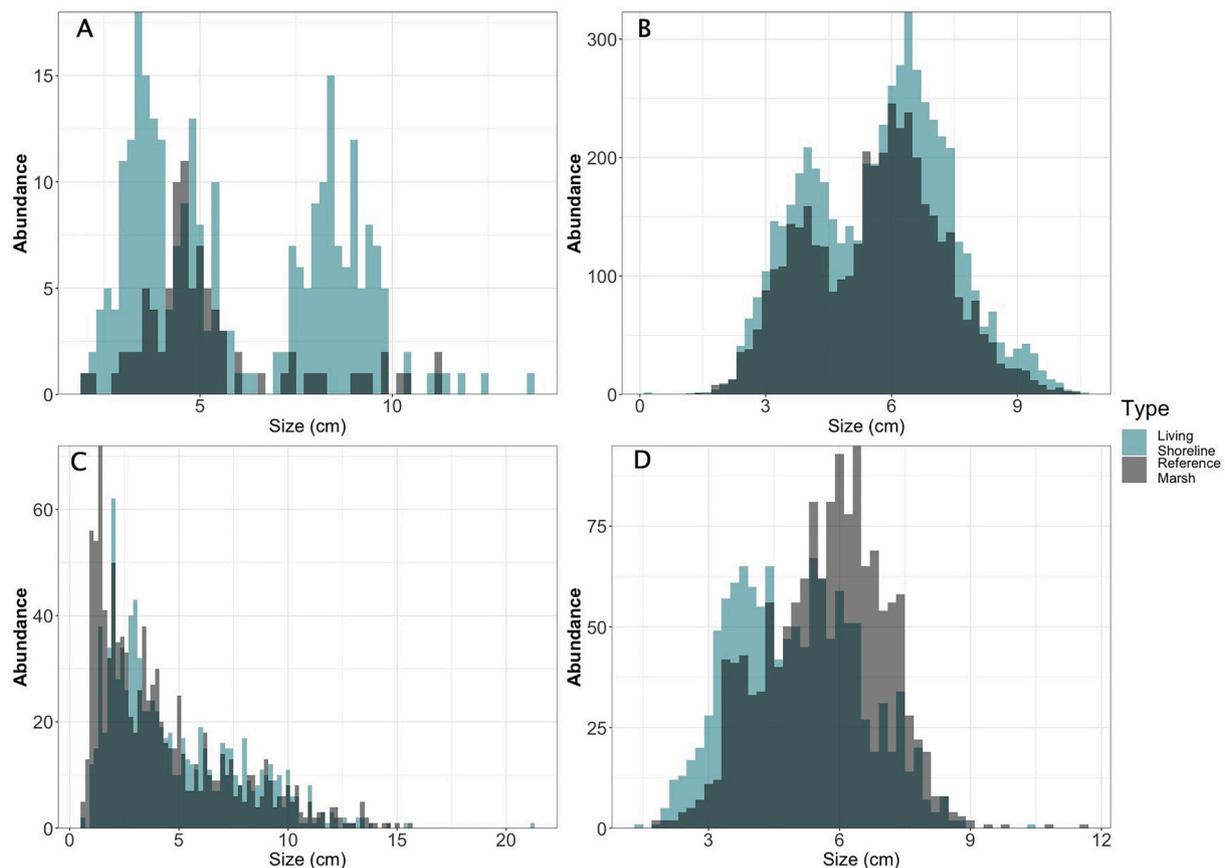
**Table 3**

Model fit and variance explained.

|                        | Marsh characteristics | Site setting          | Shoreline type      |
|------------------------|-----------------------|-----------------------|---------------------|
| Juvenile abundance     | 2.18<br>(0.15, 0.70)  | 10.39<br>(0.58, 0.58) | n/a                 |
| Forage abundance       | 14.3<br>(0.11, 0.62)  | 13.1<br>(0.30, 0.48)  | n/a                 |
| Mummichog condition    | -15.8<br>(0.01, 0.8)  | -20.6<br>(0.04, 0.14) | 9.2<br>(0.02, 0.8)  |
| Mummichog gut fullness | 36.0<br>(0.10, 0.26)  | 13.7<br>(0.05, 0.09)  | 54.7<br>(0.05, 0.9) |
| Silverside condition   | -20.6<br>(0.00, 0.6)  | -33.4<br>(0.01, 0.6)  | 20.4<br>(0.05, 0.1) |

Two models, marsh characteristics and site setting, were run for juvenile abundance and forage base abundance. These models and an additional shoreline type model were run for mummichog condition, mummichog gut fullness, and Atlantic silverside condition. The first value listed in the table is the  $\Delta AIC$ , with higher  $\Delta AIC$  values indicating a better model fit, and positive values indicating the model was a better fit than the null model. The first value in parenthesis is the  $r^2$  value for the fixed effects, which explains the variation accounted for by the fixed effects, and the second value in the parenthesis is the variation ( $r^2$ ) explained by the whole model.

For juvenile abundance, the site setting model was a much better predictor than the null model and the marsh characteristic model was marginally better than the null model ( $\Delta AIC$ , Table 3). For forage species abundance, the marsh characteristic model and site setting model were similar predictors of forage abundance and both models were better fits than the null model ( $\Delta AIC$ , Table 3). More juveniles were found at sites that had more marsh habitat nearby, i.e., lower distance to marsh



**Fig. 2.** Size-frequency comparisons.

There were differences detected for the size-frequency of striped killifish (A), mummichog (B), blue crab (C), and silverside (D) at living shorelines and reference (natural) marshes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

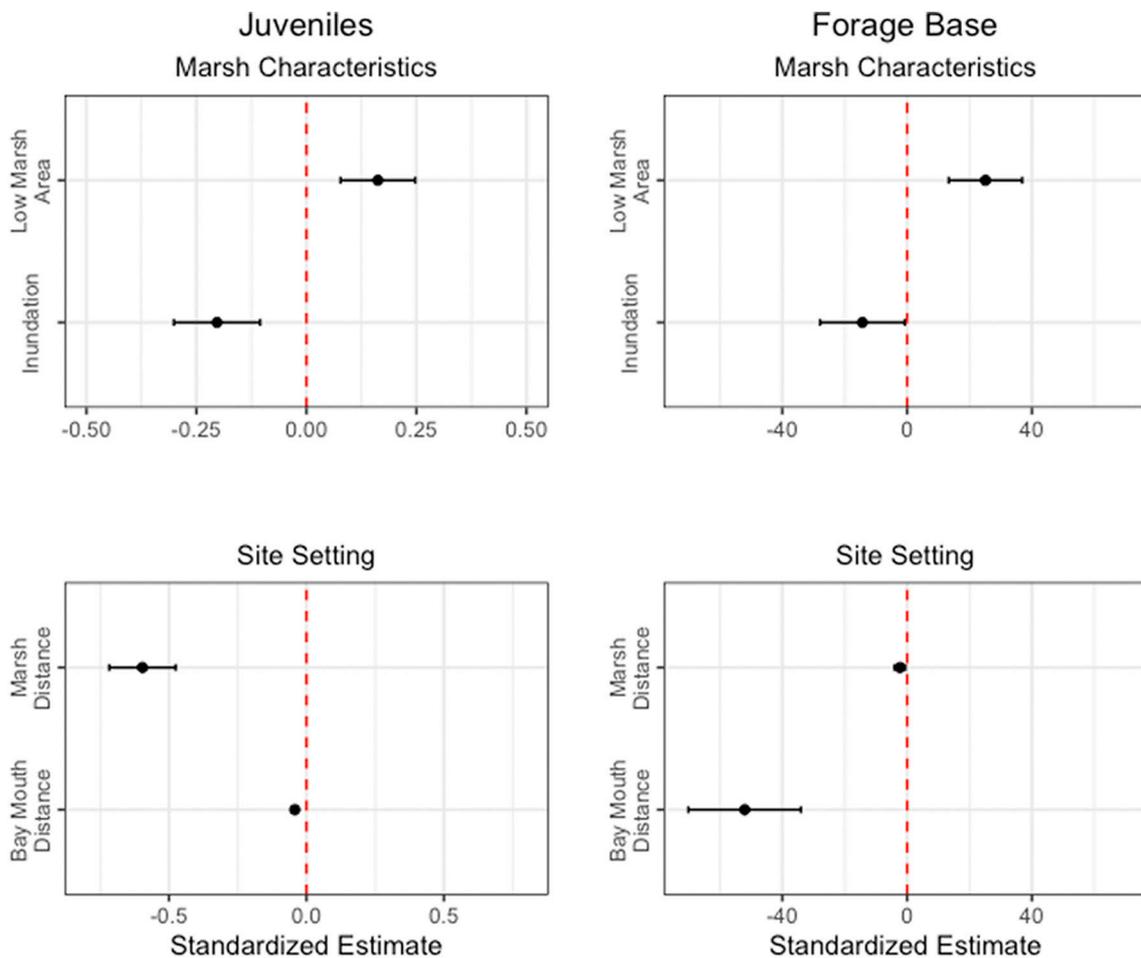


Fig. 3. Model variable effect sizes, juvenile and forage base.

Marsh characteristics and site setting models were run for juvenile abundance and forage base abundance. Independent variables were centered and standardized. The resulting coefficients reflect the effect size of each variable, plotted below with standard error bars. When the standard error bars do not include 0, that variable has a detectable effect on abundance. Coefficients below zero have an inverse relationship with abundance (e.g., sites with shorter inundation duration have higher juvenile abundance).

habitat which indicates high marsh connectivity (Fig. 3). Juveniles were more abundant at sites with a greater low marsh area, and at sites with a shorter inundation duration. Forage species were more abundant at sites with greater low marsh area, marshes with a shorter inundation duration, and sites closer to the mouth of Chesapeake Bay (Fig. 3).

The shoreline type model was the best predictor of mummichog condition (Table 3). The marsh characteristics model and the site setting model were poorer fits than the null model, and the fixed effects in these two models explained 1% and 4%, respectively, of the variation in condition. On average, mummichog had a lower condition at natural marshes in both years. Mummichog had higher condition in 2018 yet fuller guts in 2019 (Appendix: Fig. S1). The shoreline type model explained mummichog gut fullness the best, but the marsh characteristics model explained the most variation, 26% (Table 3).

Atlantic silverside condition was best predicted by the shoreline type model. The site setting and marsh characteristics models provided poorer fits than the null model (Table 3). In the shoreline type model, however, year was an important factor while shoreline type was not an important factor. Atlantic silverside had a lower mean condition in 2019 than in 2018 (Appendix: Fig. S1).

#### 4. Discussion

Overall, we found that living shorelines provide similar habitat as reference marshes based on nekton diversity, abundance, and biomass

comparisons. After 2 years since living shoreline construction, we did not detect any trend of nekton habitat use associated with living shoreline age. Juvenile nekton are using living shorelines similarly to natural marshes, while some forage base species (e.g., mummichog) have higher biomass at living shorelines. Among marshes, we found that inundation duration, low marsh, and marsh distance explained some of the variation for juvenile species and that inundation duration, low marsh, and bay mouth distance explained some of the variation in forage base species abundance. Marsh distance was a poor predictor of forage species abundance but explained juvenile abundance as marshes in more connected regions (low marsh distance) had higher juvenile abundances.

##### 4.1. Younger and older living shorelines have similar nekton use

We did not detect any relationship of nekton habitat use and living shoreline age, for living shorelines constructed at least 2 years prior to initial sampling. Similarly, Gittman et al. (2016) found that living shorelines may take up to three years for nekton establishment after living shoreline construction. They examined living shorelines constructed  $\leq 1$  and 3–8 years prior to sampling. The youngest living shoreline ( $\leq 1$ ) was not yet equivalent to the reference marsh, but the three older living shorelines sampled ( $\geq 3$  years) had equivalent or higher species diversity and abundance (Gittman et al., 2016). Our findings are similar as our sites were older than 2 years since

construction and we found that our living shoreline sites had similar abundance and diversity to reference marshes. Additional research at our study sites indicates that living shorelines reach ecological equivalency with reference marshes for other habitat use assessments (e.g., periwinkle snails *Littoraria irrorata*, diamondback terrapin *Malaclemys terrapin*, herons) after 2 years, but there is a delay in soil composition equivalency with natural marshes (i.e., phosphorus, carbon, nitrogen, organic matter, Chambers et al., 2021; Isdell et al., 2021). The delay in soil composition equivalency, relative to reference marshes, is due to the clean sand fill used to create suitable tidal elevations. As there were no trends of nekton use associated with living shoreline age, living shoreline ecosystem function, such as foraging opportunities and predator refuge, may be established early, similar to characteristics such as vegetation (Bilkovic et al., 2021; Isdell et al., 2021).

#### 4.2. Living shorelines provide suitable nekton habitat

Living shorelines support similar diversity, similar abundance, and higher biomass of marsh nekton communities compared to reference fringing marshes after two years post-construction. Living shorelines and reference marshes have similar taxonomic diversity, indicating similar habitat use patterns by functional groups across these marsh types. The higher biomass at living shorelines is likely related to differing characteristics (rock sill, soil composition) between living shorelines and natural marshes.

At these living shorelines, the rock sill provides an additional structural feature that, in the right setting, can attract fauna commonly associated with oyster reefs (Bilkovic and Mitchell, 2013). Restored or natural oyster reefs near an intertidal marsh can support a more diverse or functionally redundant nekton community (Waltham et al., 2021). Similarly, compared to natural shoreline habitats (intertidal mudflats and marshes), living shoreline marshes with rock sills tend to have higher macrobenthic invertebrate species abundance and biomass due to the addition of complex structure and interstitial niches (Bilkovic and Mitchell, 2017). The increased prevalence of macrobenthic invertebrates detected on living shoreline rock sills, particularly suspension-feeding epifauna, such as eastern oyster (*Crassostrea virginica*), mussels (*Ischadium recurvum*, *Geukensia demissa*), and barnacles (*Balanus* and *Chthamalus* spp), may contribute to increased prey availability for benthic feeders and nekton at living shorelines. Our living shorelines study sites were not adjacent to natural oyster reefs, and thus the living shoreline rock sill may be providing similar structural functions as naturally occurring oyster reefs found in other coastal regions (Waltham et al., 2021). More work is necessary to assess ecosystem service similarities between living shoreline sills and natural biogenic reefs.

A marsh sill maintains subtidal shallow water environments and supports marsh vegetation establishment, which is reflected in similarity of the nekton community structure at living shoreline and reference marsh sites. In contrast, shoreline hardening (riprap revetment, bulkhead) causes deepening of nearshore waters and elimination of intertidal and subtidal habitat, which reduces the value of shoreline habitats for refuge from predators and foraging (Balouskus and Targett, 2016; Bilkovic et al., 2006; Kornis et al., 2017). Hardened shorelines alter the shallow water nekton community from assemblages of diverse, small-bodied and juvenile species to larger, transient species (Kornis et al., 2018, 2017). Similar to other studies of nekton use of living shorelines in the Mid-Atlantic region (Balouskus and Targett, 2016; Currin et al., 2008), our study finds that the presence of a marsh sill does not substantially change the shallow water nekton community, which is predominantly made up of small-bodied or juvenile individuals common in intertidal marsh habitats. The maintenance of shallow water habitat by the marsh sill suggests that nekton habitat usage of living shoreline marshes and nearby subtidal shallow habitats are related, but the exact nature of those patterns requires additional study.

In addition to the marsh sill, habitat conditions in living shorelines

may be altered by the clean sand fill used during construction, which results in intertidal sediment composition that is looser, more granular, and less nutrient rich (Becker et al., 2017; Bilkovic and Mitchell, 2017; Chambers et al., 2021). The sand fill may contribute to altered or reduced infauna availability, as nutrient and organic matter accumulation are often delayed in created marshes (Bilkovic and Mitchell, 2013; Chambers et al., 2021), but this does not appear to affect the nekton community as there was no trend of nekton abundance associated with living shoreline age. Unexpectedly, the sandy sediment in living shoreline marshes may create alternative habitats; striped killifish prefer sandy habitat (Harvey, 1998) and were more abundant at living shorelines. Either the delayed nutrient accumulation does not substantially degrade foraging opportunities or alterations of the detrital food web may be counteracted by the presence of more fauna on the rock sill.

#### 4.3. Living shorelines provide nursery habitat comparable to reference marshes

Living shorelines provide similar estuarine nursery habitat as natural marshes (Beck et al., 2001; Minello et al., 2003; Sheaves, 2009). We found similar juvenile abundance and biomass at living shorelines and paired reference marshes. All non-forage species captured were predominantly (>90%) juveniles, which includes culturally and economically valued species, such as striped bass and spotted sea trout (*Cynoscion nebulosus*). Juvenile striped bass will forage in salt marshes, feeding on blue crabs, mummichog, and shrimp (Nemerson and Able, 2003; Tupper and Able, 2000). Juvenile spotted sea trout preferentially settle in vegetated habitats, and will use salt marshes for refuge and forage – particularly when submerged aquatic vegetation is not nearby (Baltz et al., 1998; Neahr et al., 2010). We selected sites that did not have adjacent, submerged aquatic vegetation to reduce confounding effects of other surrounding habitat types.

Juveniles find similar refuge at living shoreline and reference marshes. Sites with more marsh habitat nearby had higher abundances of juveniles, indicating living shorelines are likely contributing to shorescape connectivity and can be used to create suitable marsh habitat. Across both habitat types, more juveniles were found in sites with shorter inundation duration. Among our sites, marshes with shorter inundation times had shallower depths along the marsh edge. Shallow water limits larger piscivores from accessing the marsh, providing increased predator refuge for juvenile nekton along the intertidal marsh edge (Banikas and Thompson, 2012; Clark et al., 2003; McIvor and Odum, 1988; Ruiz et al., 1993). Juvenile nekton were more abundant at sites with larger low marsh area, indicating that more fringing edge habitat (i.e., low marsh) supports more juveniles, a pattern that has been observed in other marsh systems (Baker and Sheaves, 2005; Ruiz et al., 1993). Juvenile silversides were more prevalent at living shorelines, which can be due to the increased habitat complexity as a source of refuge and/or an attraction to the sandy sediment. Often schools of Atlantic silverside are abundant near sandy sediments or vegetated habitats, and juveniles move in and out of the marsh until they are 6–8 cm long TL (Able and Fahay, 1998). Juveniles were slightly more abundant towards the bay mouth in both living shorelines and reference marshes.

#### 4.4. Living shorelines provide similar estuarine trophic support as reference marshes

Living shorelines support similar or enhanced habitat for forage species, which ultimately can support the trophic relay of energy and nutrients out of marshes to the larger estuary (Deegan et al., 2002; Kneib and Wagner, 1994). Small-bodied littoral fish and benthivores had higher biomass at living shorelines than at reference marshes, indicating that the differences in living shoreline structure (sill, sediment composition) do not inhibit feeding opportunities for primary or secondary consumers that forage in intertidal marshes. The five species driving the

differences in biomass across shoreline type were all part of the forage base (mummichog, silverside, striped killifish, blue crab, shrimp). Two of these species, striped killifish and silverside, had different habitat use patterns based on fish age. Adult and juvenile striped killifish were more abundant at living shorelines, with few adult striped killifish at reference marshes, possibly because they prefer sandy habitat to the more organic sediment of natural marshes (Harvey, 1998). There were more juvenile than adult silverside at living shorelines, indicating that young silverside may be using living shorelines as a nursery habitat or refuge.

Adult silverside were more prevalent at reference marshes, indicating that adult silverside may be using natural marshes more often for reproduction when compared to living shoreline marshes (Balouskus and Targett, 2012; Conover and Ross, 1982). Similarly, Balouskus and Targett, 2012) found that Atlantic silverside deposit more eggs at natural shorelines than at living shorelines with a sill. On average, we found that Atlantic silverside had a slightly higher body condition in 2018, indicating that the estuarine conditions were more favorable in 2018 than in 2019. Atlantic silverside condition did not vary due to shoreline type, site setting, or marsh characteristics, indicating that both living shorelines and reference marshes are providing similar feeding opportunities and refuge habitat.

Modal size for both juvenile (<6 cm TL, (Able and Fahay, 1998) and adult mummichogs was larger at living shorelines than at reference marshes, suggesting that living shorelines provide suitable conditions for rapid growth of this marsh resident species. Mummichog are generalist benthivores that feed in intertidal marshes (Allen et al., 1994; Thompson, 2015), and adult mummichog had fuller guts and better condition at living shorelines. These differences indicate that there may be increased prey availability or prey quality at these sites. Larger mummichog (>7 cm) consume grass shrimp (*Palaemonetes* spp.; Thompson, 2015) which were often more abundant at living shorelines than at their paired reference marsh ( $180 \pm 91$  (SE) and  $120 \pm 39$  for living shorelines and reference marshes in 2018). More grass shrimp may contribute to higher mummichog gut fullness, better condition, and presumed faster growth rates at living shorelines. The presence of the living shoreline sill may also diversify prey availability for mummichogs. Crum et al. (2018) found higher mummichog growth rates along riprap revetment than along fringing marshes, and while that difference may be partially related to differences in mummichog density observed along those shoreline types, it also suggests that hardened structures, like rock sills, may provide feeding opportunities for mummichogs.

We found higher abundances of forage nekton towards the Chesapeake Bay mouth, which is consistent with other studies that demonstrate greater marine and estuarine fish abundances at higher salinities (Wagner and Austin, 1999). There is no relationship of nekton forage abundance with marsh distance, i.e., marshes in ecologically isolated and more connected marsh shorelines (often, urban and rural settings) provide similar forage habitat and estuarine trophic support, per marsh. Thus, properly designed living shorelines have the potential to provide suitable nekton forage base habitat in modified, urbanized regions. Since living shorelines provide suitable habitat for forage species, living shorelines correspondingly provide support for the detrital and marsh-based food web that supports estuarine production for commercially and culturally valued fisheries.

## 5. Conclusions

Living shoreline marshes are comparable habitat for nekton and

provide similar or improved habitat provisioning as nearby natural fringing marshes. The living shoreline nekton community is similar to the community found in reference marshes across the range of living shoreline ages in our study. The presence of small-bodied nekton and similar or higher condition for common species suggest that properly constructed living shorelines provide essential functions similar to natural marshes, including nursery habitat and foraging opportunities. Our work shows that living shoreline marsh creation and restoration efforts can supplement efforts to combat marsh habitat loss by providing essential habitat. Even in highly developed and urbanized systems, we show that small-scale living shorelines can support or enhance nekton habitat, which can help reduce the impacts of marsh habitat loss. Although the community composition abundances at living shorelines and reference marshes are similar, living shoreline marsh construction practices and differing habitat characteristics (rock sill, clean sand fill) can contribute to increased biomass for some marsh-dependent species. Compared to shoreline armoring, living shorelines are often more resilient during extreme storm events and can better protect shoreline properties as seas rise (Gittman et al., 2014; Smith et al., 2018). Living shorelines with rock sills may provide structural benefits similar to biogenic reefs, and have the potential to adapt better than natural marshes as they capture and retain sediment to accrete with sea level rise (Currin et al., 2008; Mitchell and Bilkovic, 2019; Waltham et al., 2021). Similarities between living shorelines and reference marshes identified in this study demonstrate that living shorelines also support the forage base and juvenile nekton, which in turn contributes to support of recreational and commercial fisheries, and subsequently coastal economies and communities.

## Author credit statement

AGG, DMB, MM, RC, REI helped with conceptualization, methodology, and data collection. AGG, DMB, JST, and REI helped with formal statistical analysis, validation, and visualization. AGG and DMB wrote the original draft, and AGG, DMB, MM, RC, JST, REI contributed to data interpretation, writing, editing, and final visualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix. Supplementary data

## References

- Able, K.W., Fahay, M.P., 1998. *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. Rutgers University Press, New Brunswick, N.J.
- Aho, K., Derryberry, D., Peterson, T., 2014. Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95, 631–636. <https://doi.org/10.1890/13-1452.1>.
- Allen, E.A., Fell, P.E., Peck, M.A., Gieg, J.A., Guthke, C.R., Newkirk, M.D., 1994. Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. *Estuaries* 17, 462–471. <https://doi.org/10.2307/1352676>.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, PRIMER-E.
- Babkin, B.P., Bowie, D.J., 1928. The digestive system and its function in fundulus heteroclitus. *Biol. Bull.* 54, 254–277. <https://doi.org/10.2307/1536857>.
- Baker, R., Sheaves, M., 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. *Mar. Ecol. Prog. Ser.* 291, 197–213. <https://doi.org/10.3354/meps291197>.
- Baloukus, R.G., Targett, T.E., 2012. Egg deposition by Atlantic Silverside, *Menidia menidia*: substrate utilization and comparison of natural and altered shoreline type. *Estuar. Coasts* 35, 1100–1109. <https://doi.org/10.1007/s12237-012-9495-x>.
- Baloukus, R.G., Targett, T.E., 2016. Fish and blue crab density along a riprap-sill-hardened shoreline: comparisons with *Spartina* Marsh and Riprap. *Trans. Am. Fish. Soc.* 145, 766–773. <https://doi.org/10.1080/00028487.2016.1172508>.
- Baltz, D.M., Fleegeer, J.W., Rakocinski, C.F., McCall, J.N., 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environ. Biol. Fish* 53, 89–103. <https://doi.org/10.1023/A:1007471724608>.
- Banikas, E.M., Thompson, J.S., 2012. Predation risk experienced by mummichog, *Fundulus heteroclitus*, in intertidal and subtidal salt marsh habitats. *Estuar. Coasts* 35, 1346–1352. <https://doi.org/10.1007/s12237-012-9517-8>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51, 633. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2).
- Becker, S.L., Franke, F., Gläsel, A., 2017. Regime pressures and organizational forms of community-based sustainability initiatives. *Environ. Innov. Soc. Transit.* <https://doi.org/10.1016/j.eist.2017.10.004>.
- Berman, M., Mason, P., Nunez, K., Tombleson, C., 2018. Implementing Sustainable Shoreline Management in Virginia: Assessing the Need for an Enforceable Policy. *Y Rep.* <https://doi.org/10.21220/V5NF3W>.
- Bilkovic, D.M., Mitchell, M.M., 2013. Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages. *Ecol. Eng.* 61, 469–481. <https://doi.org/10.1016/j.ecoleng.2013.10.011>.
- Bilkovic, D.M., Mitchell, M.M., 2017. Designing living shoreline salt marsh ecosystems to promote coastal resilience. In: Bilkovic, D.M., Mitchell, M., La Peyre, M., Toft, J. (Eds.), *Living Shorelines: The Science and Management of Nature-based Coastal Protection*. CRC Press, Taylor & Francis Group.
- Bilkovic, D.M., Roggero, M., Hershner, C.H., Havens, K.H., 2006. Influence of land use on macrobenthic communities in nearshore estuarine habitats. *Estuar. Coasts* 29, 1185–1195. <https://doi.org/10.1007/BF02781819>.
- Bilkovic, D.M., Mitchell, M., Mason, P., Duhring, K., 2016. The role of living shorelines as estuarine habitat conservation strategies. *Coast. Manag.* 44, 161–174. <https://doi.org/10.1080/08920753.2016.1160201>.
- Bilkovic, D.M., Isdell, R.E., Guthrie, A.G., Mitchell, M.M., Chambers, R.M., 2021. Ribbed mussel *Geukensia demissa* population response to living shoreline design and ecosystem development. *Ecosphere* 12, e03402. <https://doi.org/10.1002/ecs2.3402>.
- Blackwell, B.G., Brown, M.L., Willis, D.W., 2000. Relative weight (Wr) status and current use in fisheries assessment and management. *Rev. Fish. Sci.* 8, 1–44. <https://doi.org/10.1080/10641260091129161>.
- Bolger, T., Connolly, P.L., 1989. The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* 34, 171–182. <https://doi.org/10.1111/j.1095-8649.1989.tb03300.x>.
- CCRM, 2017. *Shoreline Permit Database*. (Virginia Institute of Marine Science, William & Mary), Gloucester Point, Virginia.
- Chambers, R.M., Gorsky, A.L., Isdell, R.E., Mitchell, M.M., Bilkovic, D.M., 2021. Comparison of nutrient accrual in constructed living shoreline and natural fringing marshes. *Ocean Coast. Manag.* 199, 105401. <https://doi.org/10.1016/j.ocecoaman.2020.105401>.
- Clark, K.L., Ruiz, G.M., Hines, A.H., 2003. Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *J. Exp. Mar. Biol. Ecol.* 287, 37–55. [https://doi.org/10.1016/S0022-0981\(02\)00439-2](https://doi.org/10.1016/S0022-0981(02)00439-2).
- Conover, D.O., Ross, M.R., 1982. Patterns in seasonal abundance, growth and biomass of the Atlantic Silverside, *Menidia menidia*, in a New England Estuary. *Estuaries* 5, 275–286. <https://doi.org/10.2307/1351750>.
- Crum, K.P., Baloukus, R.G., Targett, T.E., 2018. Growth and movements of Mummichogs (*Fundulus heteroclitus*) along armored and vegetated estuarine shorelines. *Estuar. Coasts* 41, 131–143. <https://doi.org/10.1007/s12237-017-0299-x>.
- Curran, C.A., Wainright, S.C., Able, K.W., Weinstein, M.P., Fuller, C.M., 2003. Determination of food web support and trophic position of the Mummichog, *Fundulus heteroclitus*, in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*), and restored salt marshes. *Estuaries* 26, 495–510. <https://doi.org/10.1007/BF02823726>.
- Curran, C.A., Delano, P.C., Valdes-Weaver, L.M., 2008. Utilization of a citizen monitoring protocol to assess the structure and function of natural and stabilized fringing salt marshes in North Carolina. *Wetl. Ecol. Manag.* 16, 97–118. <https://doi.org/10.1007/s11273-007-9059-1>.
- Curran, C.A., Chappell, W.S., Deaton, A., 2010. Developing alternative shoreline armoring strategies: The living shoreline approach. In: Carolina, North, Shipman, H., Dethier, M.N., Gelfenbaum, G., Fresh, K.L., Dinicola, R.S. (Eds.), *Puget Sound Shorelines and the Impacts of Armoring—Proceedings of a State of the Science Workshop*, May 2009. U.S. Geological Survey, Reston, VA, pp. 91–102.
- Davis, J.L.D., Takac, L., Schnabel, R., 2008. Evaluating Ecological Impacts of Living Shorelines and Shoreline Habitat Elements: An Example From the Upper Western Chesapeake Bay. Presented at the 2006 Living Shorelines Summit. Chesapeake Research Consortium, Williamsburg, Virginia.
- Deegan, L.A., Hughes, J.E., Rountree, R.A., 2002. Salt marsh ecosystem support of marine transient species. In: Weinstein, M.P., Kreeger, D.A. (Eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Dordrecht, pp. 333–365. [https://doi.org/10.1007/0-306-47534-0\\_16](https://doi.org/10.1007/0-306-47534-0_16).
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>.
- Forman, R.T.T., Deblinger, R.D., 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. *Conserv. Biol.* 14, 36–46. <https://doi.org/10.1046/j.1523-1739.2000.99088.x>.
- Gilby, B.L., Weinstein, M.P., Baker, R., Cebrian, J., Alford, S.B., Chelsky, A., Colombano, D., Connolly, R.M., Curran, C.A., Feller, I.C., Frank, A., Goetze, J.A., Goodridge Gaines, L.A., Hardcastle, F.E., Henderson, C.J., Martin, C.W., McDonald, A.E., Morrison, B.H., Olds, A.D., Rehage, J.S., Waltham, N.J., Ziegler, S. L., 2020. Human actions alter tidal marsh seascapes and the provision of ecosystem services. *Estuar. Coasts*. <https://doi.org/10.1007/s12237-020-00830-0>.
- Gittman, Rachel K., Peterson, Charles H., Curran, Carolyn A., Fodrie, F. Joel, Piehler, Michael F., Bruno, John F., 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications*. <https://doi.org/10.1890/14-0716>.
- Gittman, R.K., Popowich, A.M., Bruno, J.F., Peterson, C.H., 2014. Marshes with and without sills protect estuarine shorelines from erosion better than bulkheads during a Category 1 hurricane. *Ocean Coast. Manag.* 102, 94–102. <https://doi.org/10.1016/j.ocecoaman.2014.09.016>.
- Gittman, R.K., Fodrie, F.J., Popowich, A.M., Keller, D.A., Bruno, J.F., Curran, C.A., Peterson, C.H., Piehler, M.F., 2015. Engineering away our natural defenses: an analysis of shoreline hardening in the US. *Front. Ecol. Environ.* 13, 301–307. <https://doi.org/10.1890/150065>.
- Harvey, C., 1998. Use of sandy beach habitat by *Fundulus majalis*, a surf-zone fish. *Mar. Ecol. Prog. Ser.* 164, 307–310. <https://doi.org/10.3354/meps164307>.
- Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17, 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- Ihde, T.F., Houde, E.D., Bonzek, C.F., Franke, E., 2015. *Assessing the Chesapeake Bay Forage Base: Existing Data and Research Priorities* (STAC No. 15–005). Edgewater, MD.
- Isdell, R.E., Bilkovic, D.M., Guthrie, A.G., Mitchell, M.M., Chambers, R.M., Leu, M., Hershner, C., 2021. Living shorelines achieve functional equivalence to natural fringe marshes across multiple ecological metrics. *PeerJ*. <https://doi.org/10.7717/peerj.11815>.
- Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373, 299–302. <https://doi.org/10.1038/373299a0>.
- Kneib, R.T., 1986. Size-specific patterns in the reproductive cycle of the Killifish, *Fundulus heteroclitus* (Pisces: Fundulidae) from Sapelo Island, Georgia. *Copeia* 1986, 342–351. <https://doi.org/10.2307/1444995>.
- Kneib, R., Wagner, S., 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar. Ecol. Prog. Ser.* 106, 227–238. <https://doi.org/10.3354/meps106227>.
- Kornis, M.S., Breitburg, D., Baloukus, R., Bilkovic, D.M., Davias, L.A., Giordano, S., Heggie, K., Hines, A.H., Jacobs, J.M., Jordan, T.E., King, R.S., Patrick, C.J., Seitz, R. D., Soulen, H., Targett, T.E., Weller, D.E., Whigham, D.F., Uphoff, J., 2017. Linking the abundance of estuarine fish and crustaceans in nearshore waters to shoreline hardening and land cover. *Estuar. Coasts* 40, 1464–1486. <https://doi.org/10.1007/s12237-017-0213-6>.
- Kornis, M.S., Bilkovic, D.M., Davias, L.A., Giordano, S., Breitburg, D.L., 2018. Shoreline hardening affects nekton biomass, size structure, and taxonomic diversity in nearshore waters, with responses mediated by functional species groups. *Estuar. Coasts* 41, 159–179. <https://doi.org/10.1007/s12237-017-0214-5>.
- Laffaille, P., Brosse, S., Feunteun, E., Baisez, A., Lefeuvre, J.-C., 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal

- marine waters in the Mont Saint-Michel Bay. In: Amiard, J.-C., Le Rouzic, B., Berthet, B., Bertru, G. (Eds.), *Oceans, Rivers and Lakes: Energy and Substance Transfers at Interfaces*. Springer, Netherlands, Dordrecht, pp. 121–133. [https://doi.org/10.1007/978-94-011-5266-2\\_10](https://doi.org/10.1007/978-94-011-5266-2_10).
- Leonardi, N., Ganju, N.K., Fagherazzi, S., 2016. A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. *Proc. Natl. Acad. Sci.* 113, 64–68. <https://doi.org/10.1073/pnas.1510095112>.
- Lotrich, V.A., 1975. Summer home range and movements of *Fundulus Heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. *Ecology* 56, 191–198. <https://doi.org/10.2307/1935311>.
- Lotze, H.K., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809. <https://doi.org/10.1126/science.1128035>.
- McIvor, C.C., Odum, W.E., 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69, 1341–1351. <https://doi.org/10.2307/1941632>.
- Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C.G., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Mar. Ecol. Prog. Ser.* 246, 39–59. <https://doi.org/10.3354/meps246039>.
- Mitchell, M., Bilkovic, D.M., 2019. Embracing dynamic design for climate-resilient living shorelines. *J. Appl. Ecol.* 56, 1099–1105. <https://doi.org/10.1111/1365-2664.13371>.
- Mitsch, W.J., Gosselink, J.G., 2015. *Wetlands*, 5th ed. Wiley, Hoboken, NJ.
- Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., van Wesenbeeck, B.K., Wolters, G., Jensen, K., Bouma, T.J., Miranda-Lange, M., Schimmels, S., 2014. Wave attenuation over coastal salt marshes under storm surge conditions. *Nat. Geosci.* 7, 727–731. <https://doi.org/10.1038/ngeo2251>.
- Neahr, T.A., Stunz, G.W., Minello, T.J., 2010. Habitat use patterns of newly settled spotted seatrout in estuaries of the north-western Gulf of Mexico. *Fish. Manag. Ecol.* 17, 404–413. <https://doi.org/10.1111/j.1365-2400.2010.00733.x>.
- Nemerson, D.M., Able, K.W., 2003. Spatial and temporal patterns in the distribution and feeding habits of *Morone saxatilis* in marsh creeks of Delaware Bay, USA. *Fish. Manag. Ecol.* 10, 337–348. <https://doi.org/10.1046/j.1365-2400.2003.00371.x>.
- Nicholls, R.J., Hoozemans, F.M.J., Marchand, M., 1999. Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. *Glob. Environ. Chang.* 9, S69–S87. [https://doi.org/10.1016/S0959-3780\(99\)00019-9](https://doi.org/10.1016/S0959-3780(99)00019-9).
- Quan, W., Fu, C., Jin, B., Luo, Y., Li, B., Chen, J., Wu, J., 2007. Tidal marshes as energy sources for commercially important nektonic organisms: stable isotope analysis. *Mar. Ecol. Prog. Ser.* 352, 89–99. <https://doi.org/10.3354/meps07160>.
- R Core Team, 2020. *R: A language and environment for statistical computing*. In: *R Foundation for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99, 1–16.
- Sheaves, M., 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar. Ecol. Prog. Ser.* 391, 107–115. <https://doi.org/10.3354/meps08121>.
- Shepard, C.C., Crain, C.M., Beck, M.W., 2011. The protective role of coastal marshes: a systematic review and meta-analysis. *PLoS One* 6, e27374. <https://doi.org/10.1371/journal.pone.0027374>.
- Smith, C., Brandon, Puckett, Gittman, Rachel K., Peterson, Charles H., 2018. Living shorelines enhanced the resilience of saltmarshes to Hurricane Matthew (2016). *Ecol. Appl.* 0 <https://doi.org/10.1002/eap.1722>.
- Smith, C.S., Rudd, M.E., Gittman, R.K., Melvin, E.C., Patterson, V.S., Renzi, J.J., Wellman, E.H., Silliman, B.R., 2020. Coming to terms with living shorelines: a scoping review of novel restoration strategies for shoreline protection. *Front. Mar. Sci.* 7 <https://doi.org/10.3389/fmars.2020.00434>.
- Sutton-Grier, A.E., Wolk, K., Bamford, H., 2015. Future of our coasts: the potential for natural and hybrid infrastructure to enhance the resilience of our coastal communities, economies and ecosystems. *Environ. Sci. Pol.* 51, 137–148. <https://doi.org/10.1016/j.envsci.2015.04.006>.
- Thompson, J.S., 2015. Size-selective foraging of adult Mummichogs, *Fundulus heteroclitus*, in intertidal and subtidal habitats. *Estuar. Coasts* 38, 1535–1544. <https://doi.org/10.1007/s12237-014-9913-3>.
- Thrush, S.F., Hewitt, J.E., Hickey, C.W., Kelly, S., 2008. Multiple stressor effects identified from species abundance distributions: interactions between urban contaminants and species habitat relationships. *J. Exp. Mar. Biol. Ecol.* 366, 160–168. <https://doi.org/10.1016/j.jembe.2008.07.020>.
- Tupper, M., Able, K.W., 2000. Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. *Mar. Biol.* 137, 1049–1058. <https://doi.org/10.1007/s002270000421>.
- Wagner, C., Austin, H., 1999. Correspondence between environmental gradients and summer littoral fish assemblages in low salinity reaches of the Chesapeake Bay, USA. *Mar. Ecol. Prog. Ser.* 177, 197–212. <https://doi.org/10.3354/meps177197>.
- Waltham, N.J., Alcott, C., Barbeau, M.A., Cebrian, J., Connolly, R.M., Deegan, L.A., Dodds, K., Goodridge, L.A., Gilby, B.L., Henderson, C.J., McLuckie, C.M., Minello, T.J., Norris, G.S., Ollerhead, J., Pahl, J., Reinhardt, J.F., Rezek, R.J., Simenstad, C.A., Smith, J.A.M., Sparks, E.L., Staver, L.W., Ziegler, S.L., Weinstein, M.P., 2021. Tidal Marsh restoration optimism in a changing climate and urbanizing seascape. *Estuar. Coasts*. <https://doi.org/10.1007/s12237-020-00875-1>.
- Warwick, R., Clarke, K., 2001. Practical measures of marine biodiversity based on relatedness of species. *Oceanogr. Mar. Biol. Annu. Rev.* 207–231.