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Shoreline Hardening Affects Nekton Biomass, Size Structure, and Taxonomic Diversity in Nearshore Waters, with Responses Mediated by Functional Species Groups

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Abstract Coastal shoreline hardening is intensifying due to human population growth and sea level rise. Prior studies have emphasized shoreline-hardening effects on faunal abundance and diversity; few have examined effects on faunal biomass and size structure or described effects specific to different functional groups. We evaluated the biomass and size structure of mobile fish and crustacean assemblages within two nearshore zones (waters extending 3 and 16 m from shore) adjacent to

natural (native wetland; beach) and hardened (bulkhead; riprap) shorelines. Within 3 m from shore, the total fish/crustacean biomass was greatest at hardened shorelines, driven by greater water depth that facilitated access to planktivore (e.g., bay anchovy) and benthivore-piscivore (e.g., white perch) species. Small-bodied littoral-demersal species (e.g., *Fundulus* spp.) had greatest biomass at wetlands. By contrast, total biomass was comparable among shoreline types within 16 m from shore, suggesting the effect of shoreline hardening on fish biomass is largely within extreme nearshore areas immediately at the land/water interface. Shoreline type utilization was mediated by body size across all functional groups: small individuals (≤ 60 mm) were most abundant at wetlands and beaches, while large individuals (>100 mm) were most abundant at hardened shorelines. Taxonomic diversity analysis indicated natural shoreline types had more diverse assemblages, especially within 3 m from shore, although relationships with shoreline type were weak and sensitive to the inclusion/exclusion of crustaceans. Our study illustrates how shoreline hardening effects on fish/crustacean assemblages are mediated by functional group, body size, and distance from shore, with important applications for management.

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Introduction

Estuaries and coasts are among the world's most ecologically productive ecosystems, providing numerous ecosystem services benefitting society (Lotze et al. 2006; Barbier et al. 2011). Dense human populations in coastal areas continue to rapidly increase (Crossett et al. 2004), making estuarine systems especially vulnerable to human-linked stressors (Halpern

et al. 2008; Barbier et al. 2011). Among these stressors, shoreline hardening has gained notoriety for numerous adverse ecological effects (e.g., Dugan et al. 2011; Gittman et al. 2016a). Demand for shoreline hardening is driven by desire to protect coastal land from erosion, and as such, shoreline hardening will likely increase with global sea level rise (Rahmstorf 2007; Arkema et al. 2013) and increasing human populations in coastal areas (Crossett et al. 2004). Indeed, replacement of natural shoreline by hardened structures (e.g., bulkheads, seawalls, riprap revetments) is growing in coastal areas (Brody et al. 2008; Gittman et al. 2015) where natural shorelines including tidal wetlands have already incurred substantial losses (Lotze et al. 2006; Gedan et al. 2009; Barbier et al. 2011).

Until recently, available information on the ecological effects of shoreline hardening was limited (Seitz et al. 2006; Dugan et al. 2011). Over the last few years, however, numerous studies have described a suite of deleterious ecological effects. Fish (e.g., Toft et al. 2007; Bilkovic and Roggero 2008; Peterson and Lowe 2009; Kornis et al. 2017), invertebrates (e.g., Seitz et al. 2006; Bilkovic et al. 2006; Lowe and Peterson 2014), submerged vegetation (e.g., Patrick et al. 2014, 2016), and microbial communities (Tan et al. 2015) have all been shown to change over gradients of natural to altered shorelines. Shoreline hardening has also been linked to the expansion of nonindigenous plants (Vaselli et al. 2008; McCormick et al. 2010; Kettenring et al. 2015; Sciance et al. 2016) and animals (Glasby et al. 2006; Bulleri and Chapman 2010), an indirect but substantial effect. Many studies have focused on abundance and diversity patterns, and a recent meta-analysis of prior studies found 23% lower biodiversity and 45% lower organism abundance on bulkheads/seawalls relative to natural shorelines (Gittman et al. 2016a). Nevertheless, there remains an incomplete understanding of the response of fish and crustacean assemblages to shoreline hardening (Bilkovic & Roggero 2008; Strayer et al. 2012). For example, very few studies have examined how faunal biomass and size structure might be affected by shoreline hardening, although such effects may be substantial and have important implications for coastal management.

Our goal was to describe how the biomass, size structure, and diversity of nearshore fish and crustacean communities differed among hardened (bulkhead and riprap revetment) and natural (wetland (native vegetation) and beach) shoreline types. We also sought to answer two fundamental questions about potential responses to shoreline type: (1) how do responses differ among species, and (2) how do responses differ within comparatively narrow and wide definitions of the land/water interface? To answer question (1), we examined biomass, size structure, and taxonomic distinctness of all species and also examined biomass and size structure among three functional groups common to most estuarine systems. We elected to group species into functional groups such that

inference from our results could more easily transfer from our study system (Chesapeake Bay) to other systems. To answer question (2), we examined responses within two distinct ecotone widths to differentiate between waters immediately adjacent to the land/water interface (within 3 m from shore) and waters farther out from shore (within 16 m from shore). This study considers nuances of faunal response to shoreline hardening not previously addressed in most of the literature and provides a number of considerations for coastal management.

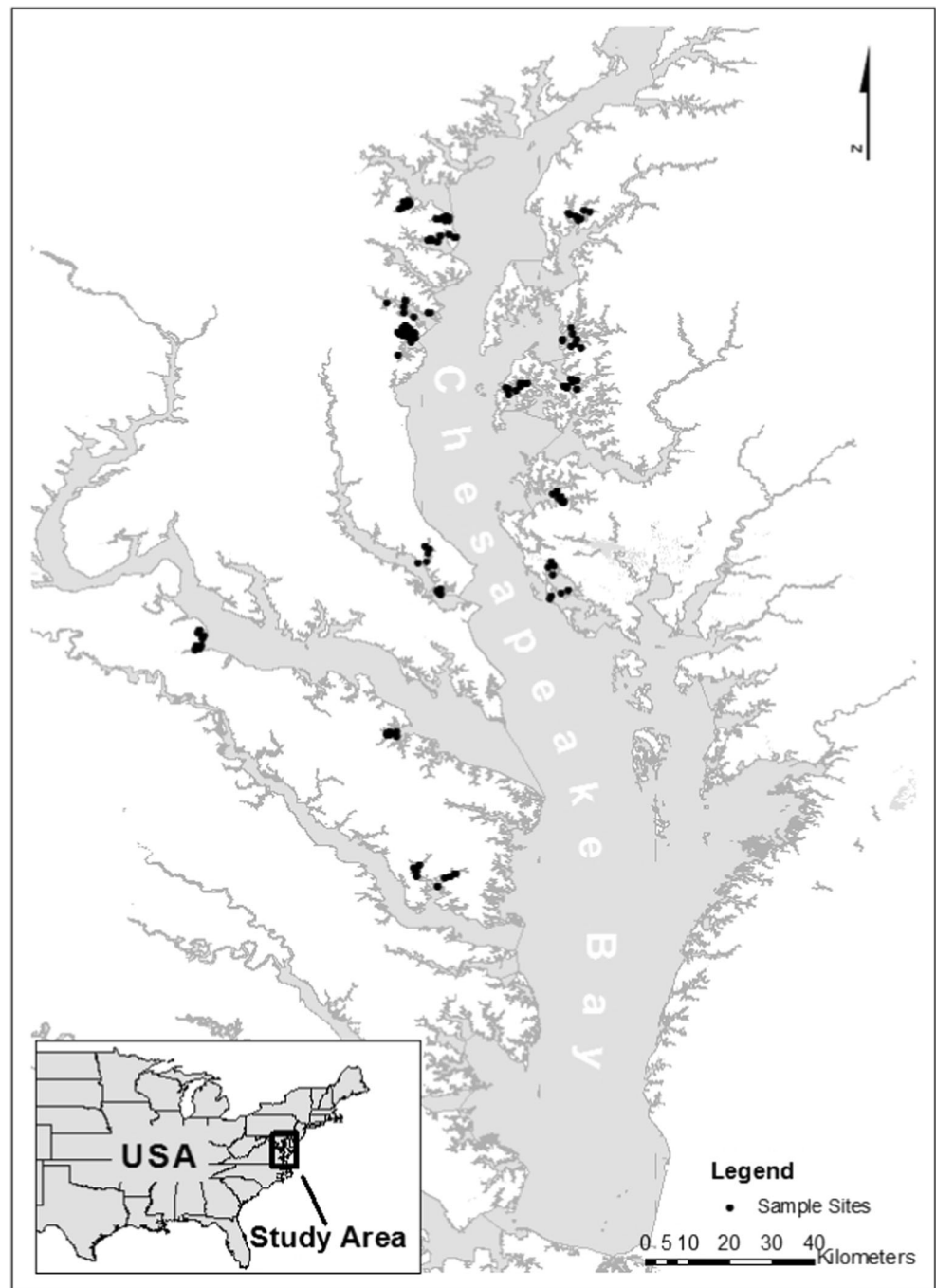
Methods

Site Selection and Study Design

We examined patterns in fish and crustacean biomass density, taxonomic distinctness, and utilization of shoreline type by size class in 16 mesohaline subestuaries (average salinity of 4–14) of the middle and upper Chesapeake Bay (Fig. 1). Here, we define “subestuaries” as independent estuaries, each with their own watershed, that feed into and interact with the larger Chesapeake Bay estuarine system; each site cluster in Fig. 1 is from a unique subestuary. Sampling occurred at two natural (wetland and beach) and two hardened (bulkhead and riprap) shoreline types prevalent in estuarine systems. Shoreline types were not sampled in proportion to their prevalence in the subestuary but rather in equal numbers within each subestuary to achieve a balanced design. Sites were selected in a randomized block design, in which sites were blocked by subestuary of capture. Although subestuarine-scale variables are not addressed in this study, subestuaries were deliberately chosen to include both highly developed (urban or agricultural land) and predominantly forested watersheds as part of a larger study focusing on shallow-water fish abundance patterns with land cover (Kornis et al. 2017). Therefore, the subestuaries in this study are representative of a wide range of conditions prevalent in the Chesapeake Bay and in other coastal systems. All fishes (common and scientific names in [Online Resource B](#)) and environmental data were collected between 31 July and 23 September in 2008 (Rhode River only), 2010, 2011, and 2012. This time window was chosen to avoid spring seasonal effects on fish and crustacean abundances, which are rather strong in Chesapeake Bay due to spring migrations of ocean-spawning species (e.g., blue crab, Atlantic croaker, spot). Although there may be temporal effects on fish and crustacean abundances within our sampling time window, these are accounted for in our analysis by treating subestuary as a blocking variable, as all sites from within the same subestuary were sampled within a few days of one another.

Shoreline-type definitions follow Davias et al. (2014). Wetlands were stands of predominantly native emergent

Fig. 1 Sample sites. Fishes were sampled in 16 subestuaries of the Chesapeake Bay at wetland, beach, bulkhead, and riprap shoreline types ($n = 188$ unique sites) from 2008 to 2012



vegetation dense enough to form a platform that is inundated at high tide. Beaches were fine or coarse sandy substrate with an absence of large woody debris, fine organic material, or dense vegetation. Bulkheads were vertical retaining walls made of wood, vinyl, metal, or concrete. Ripraps (short for “riprap revetments”) were shorelines armored primarily with large rock (>0.25 m diameter). Both bulkheads and ripraps had inundated vertical habitat at low tide, and bulkheads or ripraps that fronted wetland shorelines were excluded from sampling. Each site was located along a stretch of continuous

shoreline represented by a single shoreline type extending at least 77 m; no mixed shorelines were sampled. When possible, clusters of four sites (one of each shoreline type) were co-located within the same arm of a subestuary so that dispersal among sites within a cluster was possible for most species.

Fish Processing

Fish sampling occurred on the ebb tide within waters that extended 3 m (constant) and 16 m (on average) from shore

at each shoreline type. Both zones were sampled simultaneously at each of 72 sites (18 of each shoreline type). Areas 3 m from shore were sampled at an additional 72 sites (18 per shoreline type) and areas 16 m from shore at an additional 44 sites (11 of each shoreline type). Areas 3 m from shore were sampled using a “nested parallel” method (Kornis et al. 2017). Fifteen minutes prior to pulling nested parallel seines, three PVC poles were placed 3 m from shore to mark the sampling area. To limit disturbing the shoreline community prior to sampling, seines were floated to each site from a boat located offshore. Two 15.2 m center-bagged beach seines were set in place in tandem parallel to shore at 3 m distance. Once taut, the ends of both nets were pulled into shore simultaneously. The outer net was positioned to create a barrier, and the inner net was then pulled. The second net was pulled immediately after captured individuals were removed from the first net and placed in a bucket with ambient water for processing. Areas within 16 m of shore (16.1 ± 3.1 m (s.d.) on average, based on maximum distance of seine net bag from shore) were sampled by deploying a 61-m center-bagged beach seine by a specially designed shallow-draft skiff, with the engine mounted just aft of the bow, to maximize deployment speed (hereafter “boat-deployed” method). One person pulled one end of the big seine to shore and anchored it while the boat drove in an arc towards the second endpoint, rapidly enclosing the area to be sampled in <60 s (Supplemental Video File, video credit to H. Soulen). At sites that were simultaneously sampled at waters extending both 3 and 16 m from shore, the boat-deployed seine was set first to enclose the area. Then, after waiting 15 min to allow the site to recover from disturbance, the nested parallel seines were set and pulled as described above prior to pulling the boat-deployed seine. All seines were constructed from Delta knotless material, 4.76-mm bar mesh. For both nested parallel and boat-deployed methods, a PVC pole was used to startle fish and crustaceans hiding along the shoreline towards the net bag as the net ends were drawn together. Captured individuals were identified, and a representative random sample of up to 50 individuals per species per seine net were measured for total length to the nearest millimeter (all individuals of a species were measured if <50 were present in the net). White perch and striped bass, two species with relatively broad length ranges that often occurred at >50 per sample, were divided into two length categories (<150 mm, ≥ 150 mm) with up to 50 length measurements per category; catch in excess of 50 was also counted separately for each length category for these species. This was done to improve the biomass estimates by ensuring that representative measurements were taken at random from both large and small individuals of these species. Length categories were not needed for other species with broad length ranges (e.g., red drum, American eel) because these species were always encountered at ≤ 50 per sample and thus all individuals were measured for length.

Habitat Characteristics

Prior to sampling fauna, water temperature, salinity, and dissolved oxygen were measured from a boat at each site using a YSI 600 QS (2010–2012, $n = 144$ sites, 36 sites at each shoreline type). Sediment cores were collected for grain size analysis, and Secchi depth and volume of vegetative debris were also measured in 2011 and 2012. Six sediment cores (31.75 mm diameter PVC cut to approximately 178 mm length) were collected at each site ($n = 96$ sites, 24 of each shoreline type). Cores were collected at 3 m, 1.5 m, and as close to shore as possible on either side (laterally) of the area to be seined. All six cores were pooled into the same bag and placed immediately on ice and remained frozen until grain size analysis could be completed in the laboratory. Percent of sediment comprised of gravel (particles >2.0 mm), sand (particles 0.25–2.0 mm), and mud (particles 0.063–0.25 mm) was assessed at each site (see [Online Resource A](#) for details). Secchi depth (0.1 m increments) was measured along the shaded side of the boat prior to faunal sampling by the same individual at all sites ($n = 94$, 24 beaches and ripraps and 23 bulkheads and wetlands (failure to record Secchi depth at 1 bulkhead and 1 wetland site was an oversight)). Vegetative debris was assessed from the nested parallel beach seines only and included the following categories: coarse woody debris, coarse leafy debris, filamentous algae, sea grass, *Ulva* spp., and terrestrial debris ($n = 96$ sites, 24 of each shoreline type). The total volume of vegetative debris collected by both 15.2 m seines was roughly estimated by placing the debris into graduated cylinders for small quantities, or a 5-gal bucket marked in 0.1 L increments for large quantities of debris. Habitat characteristics were not measured in 2008 (44 sites from the Rhode River).

Redundancy analysis (RDA) and single-factor blocked ANOVAs were used to analyze relationships between shoreline type and habitat characteristics. Redundancy analysis (Borcard et al. 1992) is a direct gradient technique that partitions variation in dependent variables (i.e., habitat characteristics) into components associated with the predictors (i.e., shoreline type). Although RDA is more commonly used to understand patterns in community composition (e.g., Angermeier and Winston 1999; Sharma et al. 2011), it is useful in our application of helping to visualize how habitat characteristics vary with shoreline type and co-vary with one another. Habitat characteristic data were z-standardized for the RDA such that all data were on the same unitless scale. Average values for a given habitat characteristic across all measurements were substituted in for missing data (e.g., Secchi depth, vegetative debris, and sediment grain size for sites sampled in 2008 and 2010) such that the missing values had no effect on the RDA outcome. Redundancy analysis does

not test for statistical significance, and thus single-factor ANOVAs, blocked by subestuary of capture, were used to provide significance testing to determine whether each habitat characteristic differed among shoreline types.

Biomass Estimation

Total lengths were measured on 10,865 individuals within 3 m of shore and on 25,215 individuals within 16 m of shore, spanning a total of 49 taxa including 47 species and 2 genera. Pumpkinseed (*Lepomis gibbosus*) and bluegill (*L. macrochirus*), as well as Atlantic silverside (*Menidia menidia*) and inland silverside (*M. beryllina*), were grouped to genus due to difficulty distinguishing juveniles of these species while processing large numbers of individuals rapidly in the field. These 49 taxa were organized into functional groups based on habitat preferences and foraging behaviors (Table 1), which enabled examination of overall patterns across similar species. Unmeasured individuals in seines with >50 individuals per species were assumed to be the average length of measured individuals from that site (see equation below). Due to time constraints, grass shrimp carapace lengths were only measured on a subset of individuals ($n = 533$, collected on three dates during summer 2012 from one site and ranging from 9 to 58 mm total length), and the average length (21.2 ± 0.4 mm) was used for all unmeasured grass shrimp (equivalent to 0.082 g per individual based on length-weight relationship in Hartman and Brandt 1995). Weight (g) was estimated for each individual using established length-weight relationships (carapace width instead of length for blue crab, wingspan instead of length for Atlantic stingray) (Online Resource B). Length-weight relationships could not be found for 10 species, and substitutions were made based on taxonomy or body shape as noted in Online Resource

B (Table B1). Biomass density (g m^{-2}) for each species at each site was estimated by:

$$B = \frac{W_{\text{ave}} \times N}{A}$$

where W_{ave} is the average estimated weight (g) of measured individuals captured at that site, N is the total number of individuals caught (both measured and unmeasured), and A is the area sampled (m^2). The catchability of seine nets (i.e., the % of present individuals captured by sampling gear) differed among species, net deployment methods, and among the four shoreline types. We therefore corrected the total number of individuals caught (N in above equation) based on catchability estimates (Q values) from four-net Leslie depletions conducted at 36 sites (nine sites each of beach, bulkhead, riprap, and wetland; Kornis et al. 2017). The percentage of present individuals likely to be captured by one seine pull (Q_1) and by two seine pulls (Q_2) were used to correct boat-deployed and nested parallel seine methods, respectively (see Kornis et al. 2017 for details). This corrected for sampling bias in capture efficiency specific to each shoreline type. The nested parallel method (samples within 3 m from shore) was probably not as efficient at sampling large-bodied fish as the boat-deployed method (16 m from shore) due to greater possibility of escape along the net edges. However, this difference between nested parallel and boat-deployed methods will not affect our comparisons among shoreline types, which were performed separately for each gear type.

Utilization of Shoreline Types by Size Class

We used two-sided bootstrapped Kolmogorov-Smirnov (KS) tests ($n = 1000$ Monte Carlo simulations for each test) to

Table 1 Functional groups of studied taxa ($n = 49$), based on known habitat preferences and foraging behaviors (Murdy et al. 1997 for all finfish). The “other” functional group included unique species that

generally had very small contributions to overall biomass. Species from the “other” group were included in biomass estimates for “all species”. Scientific names are included in Online Resource B

Functional group	Description	Included species
Littoral-demersal	Small-bodied bottom-oriented species that are frequently found in extremely shallow water (<20 cm) and forage on small littoral prey. Commonly serve as prey for larger species.	Banded killifish, grass shrimp, green goby, mummichog, naked goby, rainwater killifish, striped blenny striped killifish, skillettfish, sheepshead minnow
Planktivore	Species that forage on phytoplankton and zooplankton and tend to prefer open water.	Alewife, Atlantic menhaden, <i>Menidia</i> spp., bay anchovy, gizzard shad, spottail shiner, striped anchovy
Benthivore/piscivore	Large-bodied bottom-oriented species that forage on a suite of benthic invertebrates and small fishes.	American eel, Atlantic croaker, Atlantic ray, black drum, blue crab, bluefish, brown bullhead, channel catfish, chain pickerel, common carp, hogchoker, inshore lizardfish, largemouth bass, <i>Lepomis</i> spp., red drum, silver perch, spot, spotted seatrout, striped bass, summer flounder, weakfish, white perch, yellow perch
Other	Unique species that do not readily fall into one of the other three groups.	Atlantic needlefish, harvestfish, lined seahorse, northern pipefish, northern puffer, northern searobin, striped burrfish, striped mullet

determine whether there were significant differences in the cumulative length distributions of fishes captured along the four shoreline types (Abadie 2002; Sekhon 2011). KS tests were conducted as pairwise comparisons between each unique pair of shoreline types; all species were included in the tests and separate tests were run within each distance from shore. Only individuals with field-measured lengths were used in this analysis ($n = 10,865$ within 3 m from shore and 25,215 within 16 m from shore). Unlike traditional KS analysis, the bootstrapped KS test can accommodate non-continuous distributions and point masses (i.e., data with ties; Abadie 2002; Sekhon 2011). This was important in our analysis because each length value (to the nearest 1 mm) was associated with many individual fish.

To illustrate how size classes of fish utilized different shorelines, we grouped all sampled individuals into length bins using total length and examined the total percent of catch within each bin that occurred at the each of the four shoreline types. This was done for all species in aggregate and for each of the three specified functional groups (i.e., littoral-demersal, planktivore, and benthivore-piscivore, Table 1). Most length bins were 10-mm groups, but due to a skewed size distribution within 16 m of shore, we included two 50 mm length bins for larger individuals (301–350 and 351–400 mm). All bins had ≥ 20 individuals for small nets and ≥ 50 individuals for big nets.

Taxonomic Distinctness

We used taxonomic distinctness (TD) and the variation in taxonomic distinctness (VarTD) to evaluate whether biodiversity in estuarine fauna varied along shoreline types. Taxonomic distinctness, which measures taxonomic relatedness between species pairs in each sample as the mean path length through the taxonomic tree (Clark and Warwick 1998, 2001), has several advantages over traditional diversity measures (e.g., species richness) including insensitivity to sampling effort (as shown for Chesapeake Bay fish assemblages by Tuckey and Fabrizio 2013), ability to estimate phylogenetic diversity, and being more closely linked to functional diversity (Clarke and Warwick 1999; Leonard et al. 2006; Bilkovic and Mitchell 2013). Variation in taxonomic distinctness, which is not the variance of TD among samples but rather the variation in branch lengths among all pairs of species in each sample, assesses unevenness in the taxonomic hierarchy (Clarke and Warwick 2001). Moreover, the combination of average TD and VarTD can provide an indication of the relative degradation of assemblages from different locations (Clarke and Warwick 2001). Generally, the range of average TD values is narrow for a given assemblage (e.g., fishes) from a particular study area (e.g., Ellingsen et al. 2005), and thus seemingly small numeric differences may be meaningful. Two species (blue crab and grass shrimp, Phylum Arthropoda) may have had a large influence on TD and VarTD measures due to

long path lengths with the other 39 observed species (fish, Phylum Chordata). Therefore, we estimated TD and VarTD both including and excluding the two arthropod species.

Statistical Analyses

Taxonomic distinctness and taxonomic variation were calculated using Primer version 6.1.15. analyses of variance (ANOVAs) were performed in R version 2.13.2, as were bootstrapped KS tests (function `ks.boot`, ‘Matching’ package). All ANOVAs included subestuary of capture as a blocking factor to account for possible confounding factors associated with subestuary, including date of capture, salinity, and subestuary-level differences in prey abundance, pollution, or habitat. For all statistical analyses, $\alpha = 0.05$ was used as the threshold for statistical significance. However, we also report all p values between 0.05 and 0.10 because they may indicate biologically relevant trends. Mean values are reported \pm standard error, except when noted by [s.d.] (standard deviation). Standard error was reported to assess confidence in the estimate of the mean, while standard deviation was reported to describe the magnitude of variation around the mean.

Results

Habitat Characteristics

Hardened shoreline types (i.e., bulkhead and riprap) had very similar environmental profiles, while beach and wetland habitats were more unique (Fig. 2). Water depth, Secchi depth, vegetative debris, and salinity differed significantly among shoreline types (Table 2). Water depth at 0 and 3 m from shore were positively correlated with bulkhead and riprap, while vegetative debris and Secchi depth were positively and negatively correlated, respectively, with wetlands (Fig. 2). Dissolved oxygen, water temperature, and sediment characteristics (% gravel, sand, and mud) were not significantly related to shoreline type (Table 2), although there were negative associations between percent mud and beach, and percent gravel and wetland shoreline types (Fig. 2). On average, water depth at shore was 0.51 m deeper along hardened shorelines (0.59 ± 0.03 and 0.54 ± 0.04 m at bulkheads and ripraps, respectively) than natural shorelines (0.12 ± 0.02 and 0.0 ± 0.0 at wetlands and beaches, respectively). Wetlands were also significantly deeper than beaches at shore. Water depth 3 m from shore was 0.26 m greater on average at hardened vs. natural shorelines, but water depth 16 m from shore (average distance) did not differ among shoreline types (Table 2). Secchi depth along wetland shorelines was significantly lower relative to the other three shoreline types (average difference of 0.11 m, $p < 0.006$ for all pairwise comparisons, Table 2). Wetlands also had more vegetative debris than all other habitats (Table 2, difference of 1.9 L on average, $p = 0.05$, 0.05,

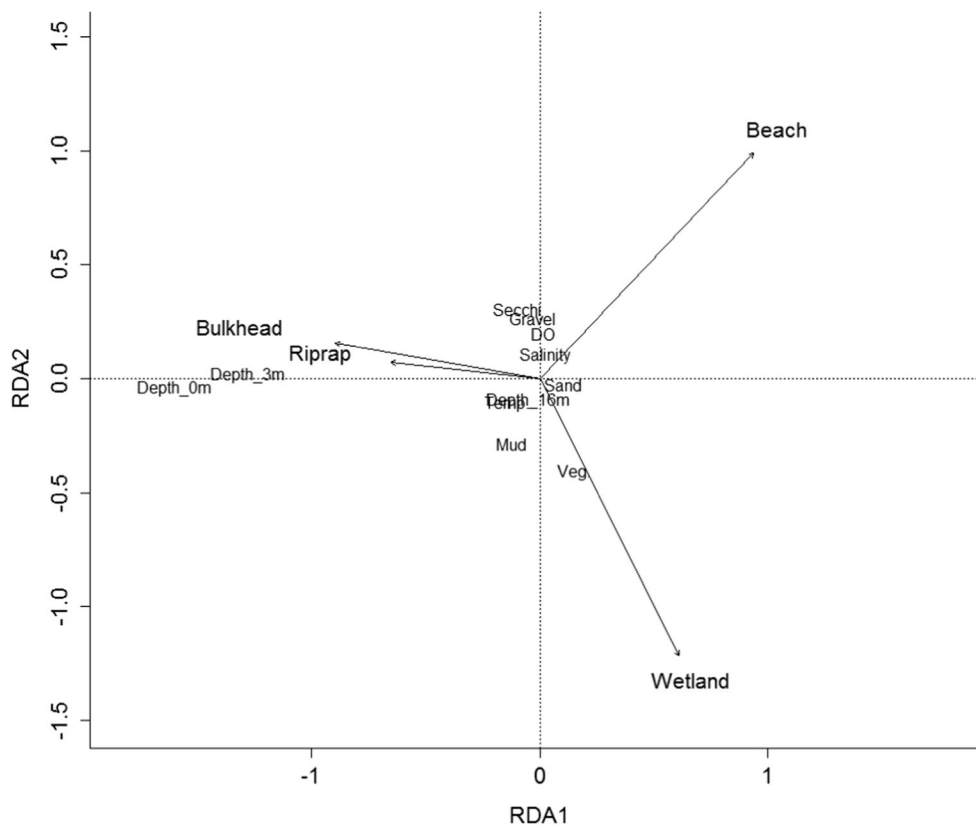


Fig. 2 Redundancy analysis (RDA) axes one and two showing associations between habitat characteristics with shoreline type. Habitat characteristics are shown in *small black letters*. *Large, bold letters and arrows* correspond with the four shoreline types. The *direction of each arrow* indicates how well each habitat characteristic correlates with shoreline type: habitat characteristics along the positive direction of each arrow (i.e., towards the point) are positively associated with that shoreline type, whereas habitat characteristics in the opposite direction

of an arrow are negatively associated. Average water temperature is abbreviated as “Temp.,” average dissolved oxygen is abbreviated as “DO,” vegetative debris is abbreviated as “Veg.,” and percent mud, gravel, and sand are abbreviated as “mud,” “gravel,” and “sand.” Overlapping habitat characteristic codes at $(-0.1, -0.1)$ are Temp. and Depth_16m. Results of significance testing for the effect of shoreline type on each habitat characteristic are available in Table 2

and 0.12 for comparisons with riprap, beach, and bulkhead, respectively). Average salinity was significantly higher at beach (11.2 ± 0.4) compared to wetland (10.8 ± 0.04) shorelines; however, this difference is not likely to be physiologically relevant to the fauna examined in this study.

Biomass Density

Effects of shoreline type on biomass density (g m^{-2}) varied among functional species groups and between waters that extended 3 and 16 m from shore. Shoreline type had a significant effect on total biomass (i.e., all species in aggregate), benthivore-piscivore biomass, planktivore biomass, and littoral-demersal biomass within 3 m of shore (Table 3, all $p \leq 0.001$). Total biomass density was largest along bulkheads compared to all other shoreline types (Fig. 3 top panel, $p < 0.0001$ for pairwise comparisons with wetland and beach; $p = 0.009$ for comparison with riprap). Total biomass density was also larger along riprap vs. beach shorelines ($p = 0.06$). This pattern was driven largely by benthivore-piscivore biomass, which accounted for

77.7% of all biomass captured within 3 m of shore and was largest along bulkhead compared to all other shoreline types ($p < 0.0001$ for pairwise comparisons with wetland and beach; $p = 0.003$ for comparison with riprap). Several taxa, including blue crab, *Lepomis* spp., spot, striped bass, and white perch contributed to larger benthivore-piscivore biomass at bulkheads. Planktivore biomass was also largest along altered shorelines (riprap > wetland ($p = 0.01$) and beach ($p = 0.04$); bulkhead > wetland ($p = 0.02$) and beach ($p = 0.07$)) within 3 m of shore, largely driven by a single taxa, *Menidia* spp. In contrast to other functional groups, littoral-demersal biomass was largest along wetlands compared to all other shoreline types (Fig. 3 top panel, $p = 0.002$, 0.002, and 0.10 in pairwise comparisons with beach, bulkhead, and riprap, respectively). Mummichog, grass shrimp, and striped killifish contributed the most to patterns in littoral-demersal species (Table 3).

Total biomass density was comparable among all four shoreline types in samples extending 16 m, on average, from shore (Table 4; $F_{3,77} = 0.3$, $p = 0.86$; Fig. 3 bottom panel); this was in contrast to patterns within 3 m of shore. The difference

Table 2 Environmental profile of beach, wetland, bulkhead, and riprap shorelines

Response	Beach	Wetland	Bulkhead	Riprap	Shoreline type effect	Blocking factor	Sig. different pairs
Dissolved oxygen ($\mu\text{g L}^{-1}$)	7.3 \pm 0.3	6.8 \pm 0.2	7.0 \pm 0.3	7.1 \pm 0.3	$F_{3,114} = 0.7, P = 0.55$	$F_{15,114} = 3.5, P < 0.0001$	
Salinity	11.2 \pm 0.4	10.8 \pm 0.4	10.9 \pm 0.4	11.1 \pm 0.4	$F_{3,125} = 3.1, P = 0.03$	$F_{15,125} = 148.5, P < 0.0001$	BC > WT
Temperature ($^{\circ}\text{C}$)	28.0 \pm 0.6	27.9 \pm 0.3	28.1 \pm 0.3	27.9 \pm 0.3	$F_{3,125} = 0.1, P = 0.98$	$F_{15,125} = 6.4, P < 0.0001$	All others > WT WT > RR & BC
Secchi depth (m)	0.59 \pm 0.06	0.47 \pm 0.04	0.57 \pm 0.05	0.58 \pm 0.04	$F_{3,80} = 7.1, P < 0.0001$	$F_{10,80} = 37.5, P < 0.0001$	
Vegetative debris (L)	0.3 \pm 0.1	2.3 \pm 1.1	0.6 \pm 0.3	0.3 \pm 0.2	$F_{3,82} = 3.2, P = 0.03$	$F_{10,82} = 2.5, P = 0.01$	
% gravel (>2.0 mm)	15.0 \pm 4.2	7.5 \pm 2.4	14.8 \pm 3.6	9.6 \pm 2.6	$F_{3,82} = 1.6, P = 0.21$	$F_{10,82} = 2.6, P = 0.009$	
% sand (0.25–2.0 mm)	81.5 \pm 4.4	81.8 \pm 3.9	77.1 \pm 4.8	81.3 \pm 3.2	$F_{3,82} = 0.3, P = 0.83$	$F_{10,82} = 1.4, P = 0.21$	
% mud (0.063–0.25 mm)	3.5 \pm 1.2	10.7 \pm 3.7	8.1 \pm 2.8	9.1 \pm 2.5	$F_{3,82} = 1.3, P = 0.29$	$F_{10,82} = 0.8, P = 0.66$	
Depth at shore (m)	0.0 \pm 0.0	0.12 \pm 0.02	0.59 \pm 0.03	0.54 \pm 0.04	$F_{3,124} = 125.8, P < 0.0001$	$F_{15,124} = 2.1, P = 0.02$	BH & RR > WT & BC; WT > BC
Depth 3 m offshore (m)	0.42 \pm 0.02	0.46 \pm 0.02	0.72 \pm 0.03	0.67 \pm 0.03	$F_{3,122} = 41.2, P < 0.0001$	$F_{15,122} = 1.7, P = 0.06$	BH & RR > WT & BC
Depth 16 m offshore (m)	0.99 \pm 0.31	1.07 \pm 0.13	1.05 \pm 0.24	1.05 \pm 0.19	$F_{3,52} = 0.2, P = 0.89$	$F_{15,52} = 3.0, P = 0.002$	

Significant effects (single-factor ANOVAs blocked by subestuary of capture) are bolded, and shoreline types that are significantly different from one another at $\alpha = 0.05$ are listed (Tukey-Kramer post-hoc pairwise comparison procedures). Values for each shoreline type are mean \pm S.E. Dissolved oxygen, salinity, and temperature were measured in 2010–2012 and are average of surface and bottom values. Water depth was also measured in 2010–2012. Depth measurements at 0 and 3 m from shore were collected during nested parallel sampling and are precise distances. Depth measurements taken at the bag of a 61-m net deployed by boat were collected at an average distance of 16.0 m from shore

Sig. significantly, BC beach, WT wetland, BH bulkhead, RR riprap

between the 16 m and extreme nearshore patterns was due to larger amounts of planktivore and benthivore-piscivore biomass at wetland and beach shorelines within 16 m of shore compared to within 3 m of shore (Fig. 2). Average planktivore biomass density increased from 1.1 to 37.4 g m^{-2} along beaches and from 0.7 to 26.0 g m^{-2} along wetlands (3 m vs. 16 m from shore for all comparisons). Similarly, average benthivore-piscivore biomass density increased from 0.3 to 15.9 g m^{-2} along beaches and from 5.0 to 21.2 g m^{-2} along wetlands. Nevertheless, benthivore-piscivore biomass density was still larger along hardened shoreline types (bulkhead > wetland and beach ($p < 0.0001$ for both); riprap > wetland ($p = 0.08$) and beach ($p = 0.02$)). Similarly, littoral-demersal biomass density remained largest along wetlands within 16 m of shore compared to all other shoreline types ($p < 0.0001$ for all pairwise comparisons). Planktivore biomass density did not vary significantly among shorelines type within 16 m of shore (Table 4).

The average proportion of fish community biomass represented by different functional groups within 3 m of shore was very different between natural and hardened shoreline types (Fig. 4). Littoral-demersal species dominated along wetland and beach shorelines (58.4 and 54.3%, respectively), while benthivore-piscivore species dominated along bulkhead and riprap shorelines (79.3 and 72.1%, respectively). In contrast, benthivore-piscivores had the greatest fraction of fish community biomass at all four shoreline types within 16 m of shore (Fig. 4, 50.3% at beaches, 53.3% at wetlands, 73.1% at ripraps, and 85.4% at bulkheads). Notably, planktivores contributed more to fish community biomass at beaches than at other shoreline types within both 3 and 16 m from shore.

Utilization of Shoreline Types by Size Class

Cumulative length distributions for all species pooled (Fig. 5) were unique for each of the four shoreline types, both within 3 m of shore (all $p < 0.0001$; Fig. 5 upper panel) and within 16 m of shore (all $p < 0.004$; Fig. 5 lower panel). However, cumulative length distributions were more similar within hardened and natural shoreline types than between them, based on the Kolmogorov-Smirnov test statistic, D , which is the maximum vertical deviation between two cumulative length distribution curves. Within 3 m from shore, bulkhead vs. riprap ($D = 0.12$) and wetland vs. beach ($D = 0.17$) were more similar than comparisons between hardened and natural shoreline types (D values ranged from 0.41 to 0.46 for the comparisons bulkhead vs. beach, bulkhead vs. wetland, riprap vs. beach, and riprap vs. wetland). Similarly, bulkhead vs. riprap ($D = 0.05$) and wetland vs. beach ($D = 0.03$) were more similar within 16 m of shore than comparisons between hardened and natural shoreline type (D values ranged from 0.20 and 0.21 for the comparisons bulkhead vs. beach, bulkhead vs. wetland, riprap vs. beach, and riprap vs. wetland). D values were also greater for comparisons within 3 m of shore than within 16 m of shore,

Table 3 Relationships between shoreline type and biomass density (g m^{-2}) in waters within 3 m of shore for commonly occurring species and functional species groups (described in Table 1)

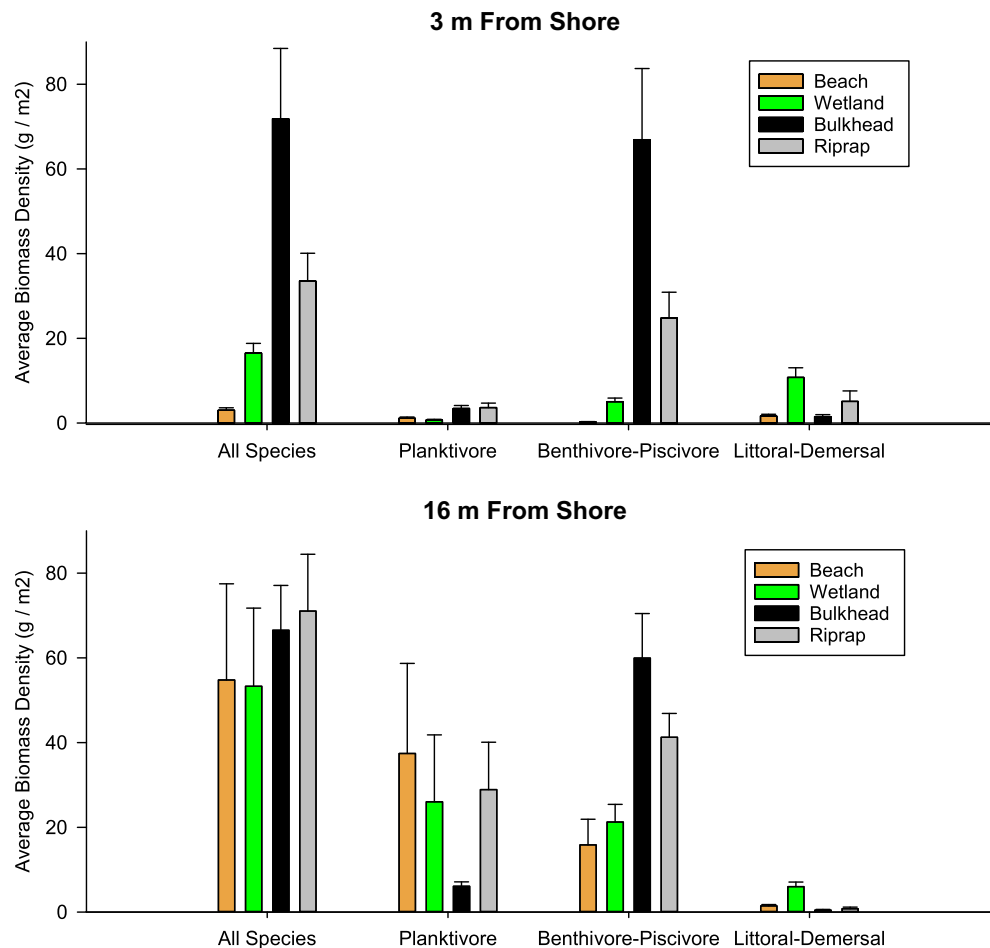
Fn. group or species	Beach	Wetland	Bulkhead	Riprap	Shoreline type effect	Blocking factor	Sig. different pairs
<i>Menidia</i> spp.	1.1 ± 0.3	0.6 ± 0.2	2.3 ± 0.5	2.6 ± 0.7	F_{3,124} = 5.2, P = 0.002	F_{15,124} = 2.1, P = 0.01	RR > WT & BC; BH > WT
Atlantic menhaden	0.0 ^a ± 0.0	0.0 ^a ± 0.0	0.6 ± 0.5	0.0 ^a ± 0.0	F _{3,124} = 1.2, P = 0.33	F _{15,124} = 1.1, P = 0.33	
Bay anchovy	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	F_{3,124} = 3.2, P = 0.03	F _{15,124} = 1.0, P = 0.42	BH > WT
Gizzard shad	0.0 ± 0.0	0.1 ± 0.1	0.4 ± 0.2	1.0 ± 0.6	F _{3,124} = 1.8, P = 0.15	F _{15,124} = 0.7, P = 0.77	
All planktivores	1.1 ± 0.3	0.7 ± 0.2	3.4 ± 0.7	3.6 ± 1.1	F_{3,124} = 5.4, P = 0.001	F _{15,124} = 1.2, P = 0.29	RR > WT & BC; BH > WT
Grass shrimp	0.0 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	F_{3,124} = 32.3, P < 0.0001	F _{15,124} = 0.8, P = 0.69	WT > all others
Mummichog	0.6 ± 0.3	5.9 ± 0.9	0.8 ± 0.4	3.6 ± 2.4	F_{3,124} = 3.6, P = 0.02	F _{15,124} = 0.5, P = 0.92	WT > BH & BC
Striped killifish	1.0 ± 0.2	2.0 ± 0.7	0.5 ± 0.2	1.1 ± 0.5	F _{3,124} = 2.1, P = 0.11	F _{15,124} = 1.0, P = 0.42	
All littoral-demersals	1.6 ± 0.4	10.8 ± 2.3	1.5 ± 0.5	5.1 ± 2.5	F_{3,124} = 6.2, P = 0.0006	F _{15,124} = 0.8, P = 0.69	WT > BH & BC
Blue crab	0.2 ± 0.1	2.7 ± 0.4	10.0 ± 1.4	6.8 ± 1.1	F_{3,124} = 21.3, P < 0.0001	F _{15,124} = 1.1, P = 0.40	BH & RR > WT & BC
<i>Lepomis</i> spp.	0.0 ± 0.0	0.6 ± 0.4	10.0 ± 4.8	3.4 ± 1.4	F_{3,124} = 3.9, P = 0.01	F_{15,124} = 2.8, P = 0.001	BH > WT & BC
Spot	0.0 ± 0.0	0.1 ± 0.1	1.7 ± 0.6	0.6 ± 0.2	F_{3,124} = 6.1, P = 0.0006	F _{15,124} = 1.6, P = 0.09	BH > WT & BC
Striped bass	0.0 ^a ± 0.0	0.0 ± 0.0	1.2 ± 0.4	0.4 ± 0.2	F_{3,124} = 3.2, P = 0.02	F _{15,124} = 1.0, P = 0.49	BH > BC
White perch	0.0 ± 0.0	1.4 ± 0.6	43.1 ± 12.1	13.1 ± 5.5	F_{3,124} = 2.8, P = 0.04	F_{15,124} = 5.0, P < 0.0001	
All ben-pisc.	0.3 ± 0.1	5.0 ± 0.9	66.9 ± 16.8	24.8 ± 6.1	F_{3,124} = 13.3, P < 0.0001	F_{15,124} = 2.6, P = 0.002	BH > all others
All species	3.0 ± 0.6	16.5 ± 2.3	71.8 ± 16.6	33.5 ± 6.6	F_{3,124} = 12.4, P < 0.0001	F_{15,124} = 2.4, P = 0.005	BH > all others

Significant effects (single-factor ANOVAs blocked by subestuary of capture) are bolded, and shoreline types that are significantly different from one another at $\alpha = 0.05$ are listed (Tukey–Kramer post-hoc pairwise comparison procedures). Values for each shoreline type are mean ± S.E

F_n: functional, Sig: significantly, BC: beach, WT: wetland, BH: bulkhead, RR: riprap

^a Denote true values of 0.0; other 0.0 values reflect rounding (e.g., average biomass density < 0.05 g m^{-2})

Fig. 3 Average biomass density (g m⁻²) of all species and three functional groups along natural (beach, wetland) and hardened (bulkhead, riprap) shoreline types. Error bars are \pm S.E. Biomasses were estimated from length data using established length-weight relationships (Online Resource B). Areas 3 m from shore were sampled by stretching two 15.2 m beach seines parallel to shore at 3 m distance, then pulling the endpoints of both nets into shore simultaneously. Areas 16 m from shore were sampled a 61-m seine deployed by boat; one person pulled one end of the big seine to shore and anchored it while the boat drove in an arc towards the second endpoint. At sites that were simultaneously sampled at both 3 and 16 m from shore, the 61-m seine was deployed first to enclose the area, and individuals captured within 3 m of shore were included in the data collected within 16 m from shore



suggesting increased similarity in cumulative length distributions at the greater distance from shore.

Shoreline type utilization was clearly related to body size within 3 m of shore, with percent of catch at hardened shorelines increasing with body size (Fig. 6). Approximately 90% of all individuals ≤ 40 mm were captured at either wetland or beach shorelines, while approximately 90% of all individuals ≥ 115 mm were captured at either bulkhead or riprap shorelines. This pattern held true for all functional species groups. For example, even though the average biomass densities of benthivore-piscivores and planktivores were significantly greater at hardened shorelines within 3 m of shore (Fig. 3, Table 3), approximately 60% of benthivore-piscivores (Fig. 6 lower left panel) and planktivores (Fig. 6 upper right panel) ≤ 50 mm were captured along natural shorelines. Most small benthivore-piscivores were captured along wetlands, while most small planktivores were captured at beaches. Similarly, approximately 65% of littoral-demersal individuals > 100 mm were captured at hardened shorelines, especially riprap (Fig. 6 lower right panel), despite significantly greater biomass density of littoral-demersals at wetland habitats (Fig. 3, Table 3). In fact, the percent of littoral-demersals captured at riprap shorelines started to increase for individuals > 70 mm.

Patterns between body size and shoreline type within 16 m of shore were similar to the patterns observed within 3 m of shore in that smaller individuals were most abundant at natural shorelines and larger individuals at hardened shorelines, but differences between shoreline types were much less distinct. Approximately 65% of all individuals ≤ 40 mm were captured at either wetland or beach shorelines, while approximately 50–70% of individuals ≥ 100 mm were captured along either bulkhead or riprap shorelines (Fig. 7 upper left panel); benthivore-piscivore species followed a similar pattern (Fig. 7 lower left panel). Planktivore patterns were highly variable, and two planktivore size classes (90–140 and 180–240 mm) were strongly associated with natural shorelines. Post-hoc analyses suggested these size classes were predominantly Atlantic menhaden (approximately 75 and 65% for the smaller and larger size ranges, respectively). Littoral-demersal species of all sizes were overwhelmingly captured along natural shorelines within 16 m of shore (Fig. 6 lower right panel).

Taxonomic Distinctness—All Species

Shoreline type had a significant effect on taxonomic distinctness (TD) both within 3 m of shore ($F_{3,124} = 5.5$, $p = 0.001$)

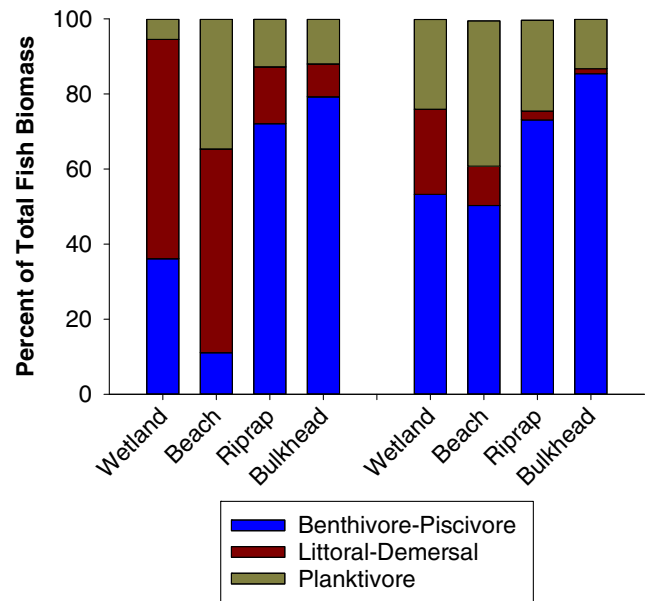
Table 4 Relationships between shoreline type and biomass density (g m^{-2}) in waters within 16 m of shore for commonly occurring species and functional species groups (described in Table 1)

Fn. group or species	Beach	Wetland	Bulkhead	Riprap	Shoreline type effect	Blocking factor	Sig. different pairs
<i>Menidia</i> spp.	2.3 ± 0.5	1.1 ± 0.4	1.3 ± 0.3	1.5 ± 0.4	$F_{3,77} = 2.0, P = 0.13$	$F_{15,77} = 1.5, P = 0.13$	
Atlantic menhaden	31.9 ± 21.3	22.0 ± 15.9	1.7 ± 0.9	23.1 ± 11.1	$F_{3,77} = 0.7, P = 0.53$	$F_{15,77} = 0.6, P = 0.86$	
Bay anchovy	1.0 ± 0.6	0.5 ± 0.2	0.4 ± 0.1	0.2 ± 0.1	$F_{3,77} = 1.2, P = 0.32$	$F_{15,77} = 1.3, P = 0.21$	
Gizzard shad	1.9 ± 0.8	2.3 ± 0.8	2.7 ± 0.7	4.1 ± 1.3	$F_{3,77} = 1.5, P = 0.23$	$F_{15,77} = 3.7, P < 0.0001$	
All planktivores	37.4 ± 21.3	26.0 ± 15.8	6.1 ± 1.1	28.9 ± 11.2	$F_{3,77} = 0.8, P = 0.50$	$F_{15,77} = 0.6, P = 0.83$	
Grass shrimp	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	$F_{3,77} = 12.0, P < 0.0001$	$F_{15,77} = 1.4, P = 0.15$	WT > all others
Mummichog	0.1 ± 0.0	2.9 ± 0.7	0.1 ± 0.0	0.1 ± 0.1	$F_{3,77} = 13.9, P < 0.0001$	$F_{15,77} = 0.5, P = 0.95$	WT > all others
Striped killifish	1.3 ± 0.3	2.7 ± 0.7	0.3 ± 0.1	0.6 ± 0.3	$F_{3,77} = 7.6, P = 0.0001$	$F_{15,77} = 2.0, P = 0.03$	WT > BH & RR
All littoral-demersals	1.4 ± 0.3	6.0 ± 1.1	0.4 ± 0.2	0.8 ± 0.4	$F_{3,77} = 20.5, P < 0.0001$	$F_{15,77} = 1.6, P = 0.09$	WT > all others
Blue crab	1.5 ± 0.2	2.8 ± 0.5	5.9 ± 1.0	6.0 ± 1.3	$F_{3,77} = 8.2, P < 0.0001$	$F_{15,77} = 2.5, P = 0.005$	BH & RR > WT & BC
<i>Lepomis</i> spp.	0.4 ± 0.3	0.6 ± 0.4	3.9 ± 1.9	1.5 ± 0.8	$F_{3,77} = 4.3, P = 0.007$	$F_{15,77} = 6.3, P < 0.0001$	BH > WT & BC
Spot	1.3 ± 0.4	3.0 ± 0.9	7.8 ± 1.9	7.7 ± 1.6	$F_{3,77} = 8.5, P < 0.0001$	$F_{15,77} = 3.4, P = 0.0002$	BH & RR > WT & BC
Striped bass	0.8 ± 0.4	0.4 ± 0.2	2.3 ± 0.9	4.4 ± 2.7	$F_{3,77} = 1.9, P = 0.14$	$F_{15,77} = 1.9, P = 0.03$	
White perch	11.3 ± 5.5	12.0 ± 4.0	37.1 ± 9.0	18.1 ± 3.9	$F_{3,77} = 5.3, P = 0.002$	$F_{15,77} = 2.8, P = 0.002$	BH > all others
All ben.-pisc.	15.9 ± 6.1	21.2 ± 4.2	60.0 ± 10.5	41.2 ± 5.6	$F_{3,77} = 11.7, P < 0.0001$	$F_{15,77} = 3.5, P = 0.0001$	BH > WT & BC; RR > BC
All species	54.8 ± 22.7	53.3 ± 18.4	66.5 ± 10.6	71.0 ± 13.4	$F_{3,77} = 0.3, P = 0.86$	$F_{15,77} = 0.8, P = 0.65$	

Significant effects (single-factor ANOVAs blocked by subestuary of capture) are bolded, and shoreline types that are significantly different from one another at $\alpha = 0.05$ are listed (Tukey-Kramer post-hoc pairwise comparison procedures). Values for each shoreline type are mean ± S.E

F_n: functional, *Sig.*: significantly, *BC*: beach, *WT*: wetland, *BH*: bulkhead, *RR*: riprap

Fig. 4 The average percentage of total fish community biomass represented by different functional groups within 3 m of shore and 16 m of shore. Areas 3 m from shore were sampled by stretching two 15.2 m beach seines parallel to shore at 3 m distance, then pulling the endpoints of both nets into shore simultaneously. Areas 16 m from shore were sampled a 61-m seine deployed by boat



and within 16 m of shore ($F_{3,77} = 4.5$, $p = 0.006$) when all species were included. Interestingly, TD patterns were opposite in waters extending 3 m and 16 m from shore: beaches had the lowest TD within 3 m of shore, but the highest TD (barely) within 16 m of shore. Within 3 m of shore, there was significantly less TD along beach shorelines (66.5 ± 4.0) compared to wetland (76.2 ± 0.8 , $p = 0.006$), riprap (76.9 ± 1.0 , $p = 0.003$), and bulkhead (74.9 ± 1.1 , $p = 0.02$) shorelines (Fig. 8, upper left panel). TD along wetland, riprap, and bulkhead shoreline types was comparable (all $p > 0.89$). Within 16 m of shore, TD was significantly lower along riprap revetments (69.4 ± 0.05) than along wetlands (71.3 ± 0.5 , $p = 0.04$) and beaches (71.7 ± 0.06 , $p = 0.01$) (Fig. 8). Average TD was also higher along beaches and wetlands than bulkheads (70.0 ± 0.7), but these difference were not statistically significant ($p = 0.10$ and 0.27 for comparisons between bulkhead vs. beach and wetland, respectively). Shoreline type also had a significant effect on taxonomic variation (VarTD) within 3 m of shore ($F_{3,124} = 5.0$, $p = 0.003$) but not within 16 m of shore ($F_{3,77} = 0.68$, $p = 0.57$). This pattern was driven by greater VarTD along wetland shorelines (552.7 ± 28.3) compared to beach (377.5 ± 47.8 , $p = 0.001$), bulkhead (445.8 ± 28.6 , $p = 0.09$), and riprap (449.7 ± 26.4 , $p = 0.11$) shorelines.

Taxonomic Distinctness—Finfish only

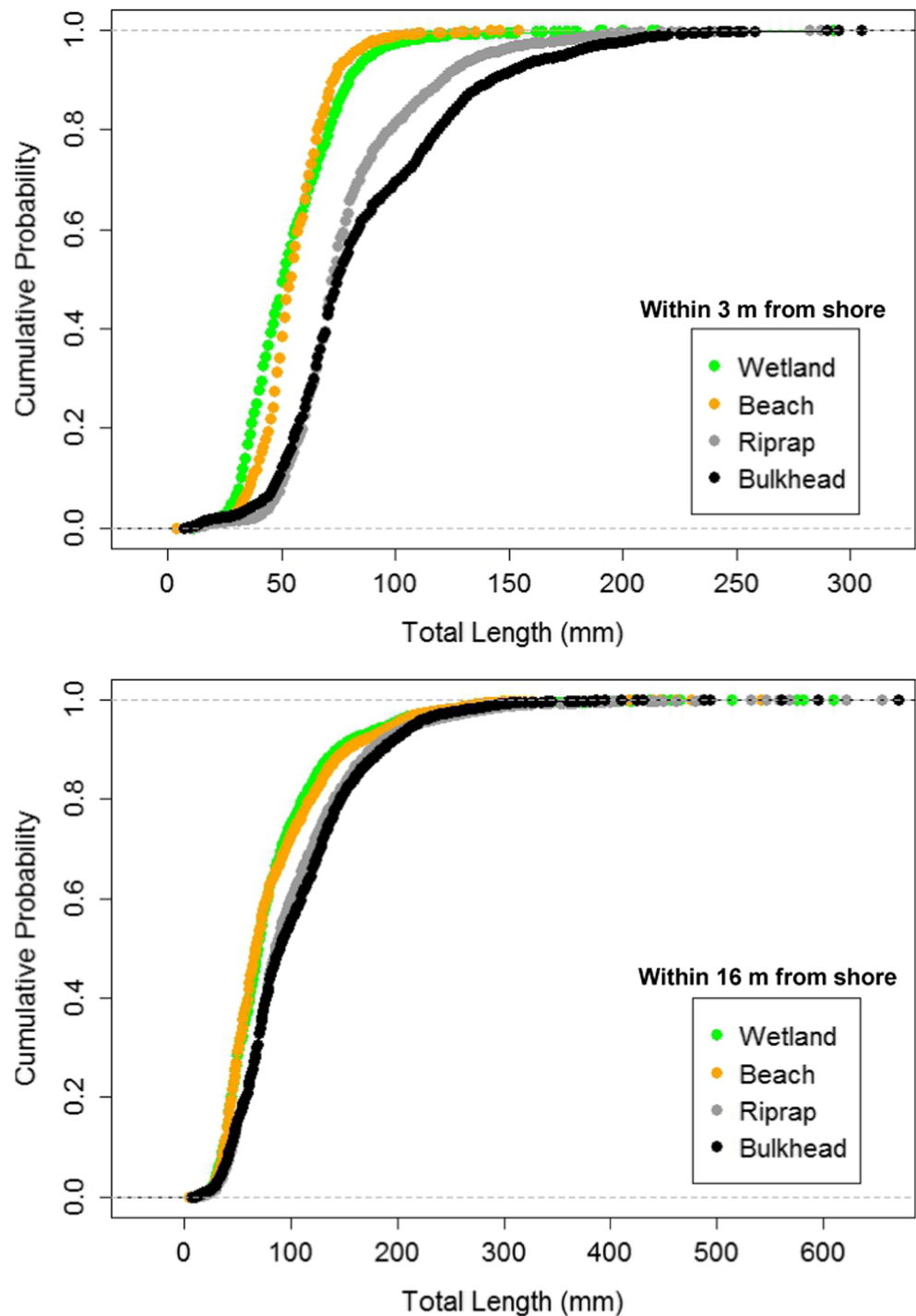
Two crustacean species (blue crab and grass shrimp) accounted for much, but not all, of differences in TD and VarTD among shoreline types. The general relationship between TD and shoreline type was the same when these two crustaceans were excluded (i.e., only finfish considered in the analysis; Fig. 8), but statistical support was not as strong for fish assemblages within 3 m of shore ($F_{3,124} = 2.4$, $p = 0.07$) or 16 m of shore ($F_{3,77} = 2.64$,

$p = 0.056$). Pairwise comparisons within 3 m of shore were similar, with less TD along beach shorelines (51.1 ± 3.7) than riprap (58.7 ± 1.8 , $p = 0.09$) wetland (58.1 ± 1.1 , $p = 0.14$) and bulkhead (58.0 ± 1.9 , $p = 0.15$) shorelines. Within 16 m of shore, finfish TD was generally comparable among shoreline types, but tended to be greater along beach (62.2 ± 0.3) and wetland (61.8 ± 0.2) shorelines than bulkhead (61.1 ± 0.4) or riprap (61.3 ± 0.3) shorelines; only the comparison between beach and bulkhead had a $p < 0.1$ ($p = 0.06$). VarTD at wetlands within 3 m from shore changed substantially with the exclusion of crustaceans. Nonetheless, VarTD of finfish tended to differ among shoreline types within 3 m of shore ($F_{3,124} = 2.3$, $p = 0.08$) but not within 16 m of shore ($F_{3,77} = 0.46$, $p = 0.71$). Finfish VarTD was higher along natural shorelines (wetland = 224.5 ± 23.6 ; beach = 211.8 ± 34.4) than hardened shorelines (bulkhead = 167.3 ± 19.8 ; riprap = 145.5 ± 23.8), but no pairwise comparison was significant (lowest p was 0.11 for the comparison between wetland and riprap).

Discussion

Our results indicate that the response of estuarine fish and crustacean biomass and size structure to shoreline hardening varies substantially among functional groups, and also by the width of the land/water ecotone considered. The likelihood of species-group-specific responses to shoreline hardening has been hypothesized by others (e.g., Munsch et al. 2016; Gittman et al. 2016a) but has largely been overlooked in empirical analyses—in part because information on the ecological effects of shoreline hardening has been sparse until very recently (Dugan et al. 2011). As a result, earlier works on fish and crustaceans emphasized broad-brush effects on total

Fig. 5 Cumulative length distributions along wetland, beach, riprap, and bulkhead shoreline types. All species and functional groups are included



abundance and diversity (Gittman et al. 2016a) and effects on small-bodied and juvenile fish most likely to be affected by disruption to natural shorelines (e.g., Peterson et al. 2000; Rozas et al. 2007). These works contributed substantially to our understanding of how shoreline hardening affects estuarine fauna, but our study offers an improved understanding of the nuances of shoreline type effects, with important applications for management.

The biomass response of littoral-demersal species to shoreline hardening that we found was consistent with prior studies, but the high amounts of benthivore-piscivore and planktivore biomass at bulkheads relative to other shoreline types contrasted with general findings on total species abundance. A recent meta-analysis of 54 published studies found a substantial effect of bulkheads/seawalls on flora, benthic infauna, birds, epibiota, and nekton, noting 23% lower biodiversity and

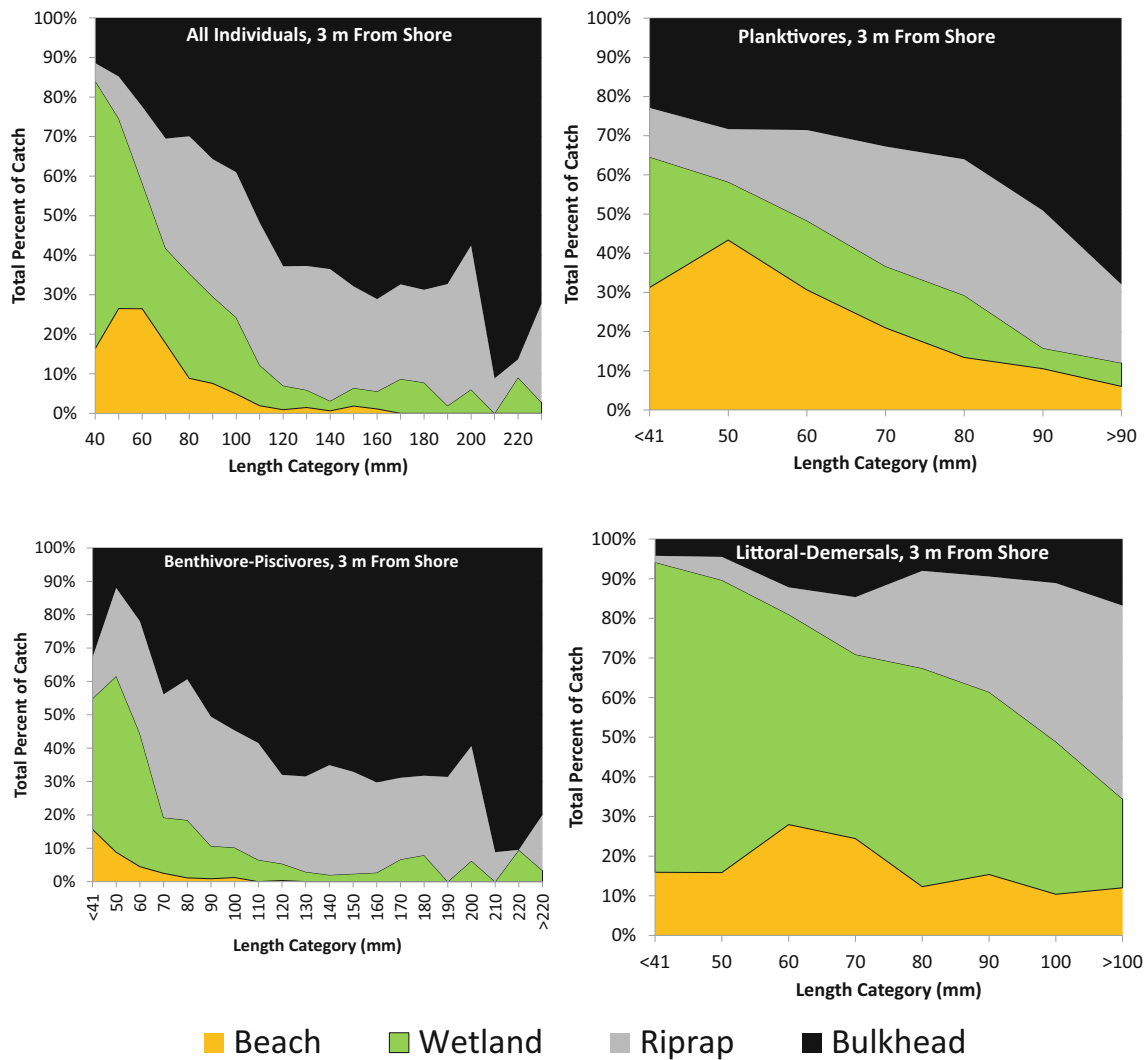


Fig. 6 Utilization of waters within 3 m of natural (wetland, beach) and hardened (bulkhead, riprap) shoreline types by fishes of different size classes, measured by percent of catch. The border line of the gray and green areas reflects the total percent of catch from natural shoreline types. All sampled individuals are grouped into 10 mm length bins, and each bin is represented along the x-axes by the upper limit (e.g., “60” refers to individuals that are 51–60 mm). The lowest size bin in all panels contains

individuals that are 0–40 mm. The upper size bin varied by species group in order to maintain at least 20 individuals in each length bin, and thus the x-axes are not consistent among panels. The upper size bin in the panels for all individuals and for benthivore-piscivores contains individuals >220 mm, compared to >90 mm for planktivores and >100 mm for littoral-demersals. As a result, patterns for all individuals are driven predominantly by benthivore-piscivores at lengths >100 mm

45% lower organism abundance relative to natural shorelines (Gittman et al. 2016a). Although these general patterns are important, both biomass (this study) and abundance (Munsch et al. 2015; Kornis et al. 2017) data indicate that the response to shoreline hardening varies substantially among species. Earlier studies have also documented this variability in the context of resident vs. transient species. Lowe and Peterson (2014), for example, found that small-bodied resident species are more negatively impacted by wetland fragmentation and loss to hardened structures than transient species that can easily move between locations (Lowe and Peterson 2014). This finding is consistent with our observations of strongly reduced biomass of small-bodied littoral-demersal species, which include several wetland residents (e.g.,

mummichog, striped killifish, grass shrimp), but increased biomass of more transient species comprising the benthivore-piscivore group (e.g., spot, striped bass, blue crab) along bulkheads and riprap revetments.

Although functional-group-specific responses to shoreline type were important, patterns in size-class-specific utilization of shoreline type superseded functional group-specific biomass responses—particularly within the extreme nearshore zone within 3 m of the shoreline. Cumulative length distributions were significantly different among all shoreline types. However, the magnitude of difference was much greater between hardened and natural shoreline types than between shoreline types within the hardened (i.e., bulkhead vs. riprap) or natural (i.e., wetland vs. beach) shoreline groups. Large

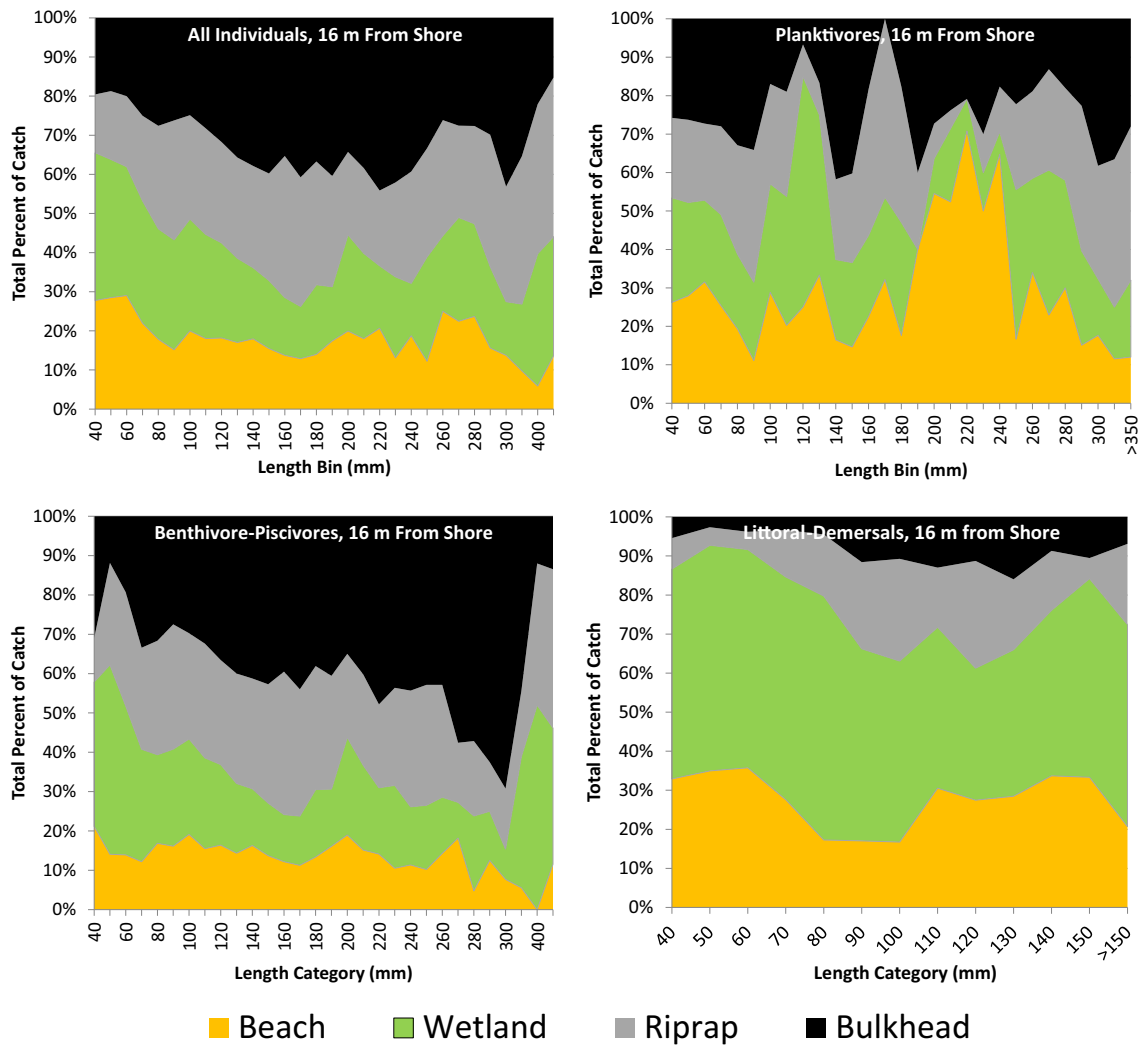


Fig. 7 Utilization of waters within 16 m of shore (on average) of natural (wetland, beach) and hardened (bulkhead, riprap) shoreline types by fishes of different size classes, measured by percent of catch. The border line of the gray and green areas reflects the total percent of catch from natural shoreline types. Sampled individuals are grouped into 10 mm length bins, except for two 50 mm length bins (301–350 and 351–400 mm) for larger sizes. Each bin is represented along the x-axes by the upper limit (e.g., “60” refers to individuals that are 51–60 mm). The lowest size bin in all panels contains individuals that are

0–40 mm. The upper size bin varied by species group in order to maintain at least 50 individuals in each length bin, and thus the x-axes are not consistent among panels. The upper size bin in the panels for all individuals and for benthivore-piscivores contains individuals >400 mm, compared to >350 mm for planktivores and >150 mm for littoral-demersals. As a result, patterns for all individuals are driven predominantly by benthivore-piscivores and planktivores at lengths >150 mm

sample sizes may also have contributed to statistically significant differences among similar cumulative length distributions for wetland vs. beach and bulkhead vs. riprap. Differences between hardened vs. natural shoreline types, rather than within each type, are therefore likely to have the greatest biological importance and are the focus of our discussion.

Small individuals of every functional group were more abundant along natural shoreline types, supporting findings of a plethora of studies documenting the importance of natural shorelines, especially wetlands, as nursery habitats (e.g., Beck et al. 2001; Minello et al. 2003; Rozas et al. 2007; Sheaves et al. 2015). Even benthivore-piscivores, whose biomass was

largely associated with bulkhead and riprap shorelines, were most often found along natural shorelines at small sizes, consistent with earlier studies (e.g., Hodson et al. 1981; Ross 2003; Nemerson and Able 2003, 2004; Able et al. 2012) including one showing that fish transitioned from extreme shallows to deeper waters as they grew (Munsch et al. 2016). Similarly, larger-bodied individuals of all functional groups were more likely to be encountered at hardened shoreline types. Although this pattern was driven by benthivore-piscivores and planktivores for individuals >150 mm in size, even littoral-demersal species show this pattern for larger individuals within that species group (90–150 mm) that

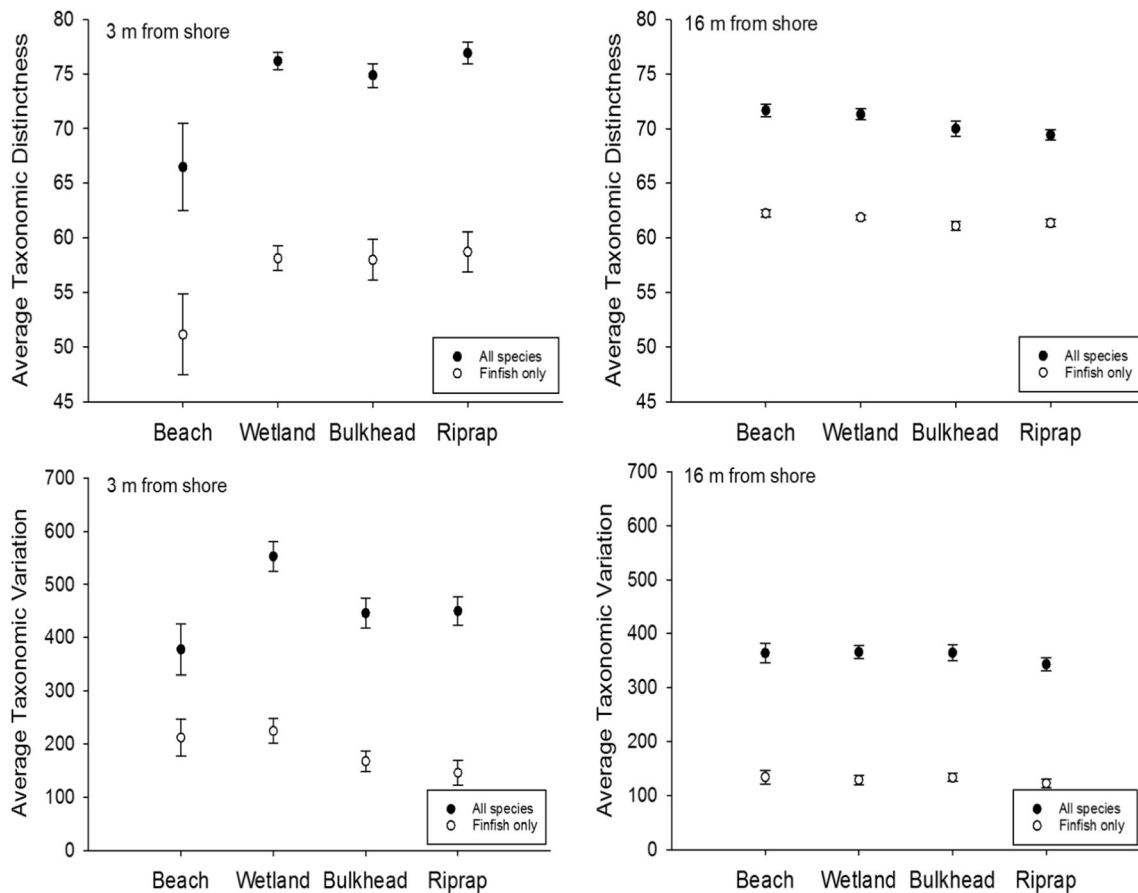


Fig. 8 Average taxonomic distinctness (*upper panels*) and taxonomic variation (*lower panels*) along four commonly occurring shoreline types. Closed black circles include all taxa (both finfish and crustaceans), while open white circles include only finfish species. Error bars are \pm S.E.

predominantly associated with riprap habitat. These findings suggest the heavy utilization of hardened shorelines by some functional groups may be at least partially dependent upon the existence of nursery and refuge habitat provided by natural shorelines, a hypothesis consistent with many earlier works showing the integration of nursery production to broader systems (e.g., Childers et al. 2000; Weinstein et al. 2005; Sheaves et al. 2015). Moreover, a study from Puget Sound noted similar effects of shoreline hardening on fish size distributions (Munsch et al. 2016), suggesting shoreline hardening effects on fish size distribution—including predation risk as perceived by fish (see below)—may be generalizable among systems.

The fact that size-class-specific shoreline utilization patterns were much stronger within 3 m of shore compared to 16 m of shore suggests a mechanism of shoreline hardening largely specific to waters immediately at the land/water interface. We argue that this mechanism is most likely increased water depth and the elimination of shallow-water habitat at hardened shorelines. Average depth at shore for both bulkhead and riprap habitats was over 0.5 m, and vertical bulkhead and riprap habitats were inundated even at low tide. The exclusion

of shallow-water habitat, including horizontal intertidal areas in marine systems, substantially reduces the value of near-shore habitat as refuge from predators. Prior studies have noted the importance of shallow-water habitat for predation refuge, and by extension, the increased predation risk associated with deeper waters (Ruiz et al. 1993; Hines and Ruiz 1995; Patterson and Whitfield 2000). Water depth/intertidal habitat also likely explained the strong association of littoral-demersal biomass with natural shorelines. Small resident fishes have repeatedly been shown to prefer shallow water, and large predatory species to prefer deep water (Akin et al. 2003; Ng et al. 2007), although Becker and Suthers (2014) found predatory species tend to increase their presence in shallow habitats (\approx 1 m deep) at night.

Size-class utilization patterns may also be driven by environmental characteristics or food availability. We found that wetland shorelines had reduced water clarity and greater amounts of vegetative debris, both of which enhance the value of wetland habitats as refuge for small-bodied individuals, especially from visual predators. In addition, Bilkovic and Roggero (2008) found greater amounts of subtidal benthic structure (e.g., shellfish beds, woody debris) along wetland

shorelines. Natural shorelines with shallow waters also have ample sources of food for small-bodied or juvenile fish (Seitz et al. 2006; Sobocinski et al. 2010). Both gut contents and stable isotope signatures, which can reflect feeding in wetland areas even at small spatial scales (Davias et al. 2014), suggest juvenile benthivore-piscivores from a variety of species including Scianoids and Moronids feed in wetland areas (Able et al. 2001; Nemerson and Able 2003, 2004; Weinstein et al. 2010). For example, spot undergo an ontogenetic diet shift from planktivores as postlarvae to benthic feeders as juveniles, and during this critical transition spot typically feed in shallow intertidal wetland habitats (Hodson et al. 1981), where both zooplankton (David et al. 2016) and benthic invertebrates (King et al. 2005; Seitz et al. 2006; Bilkovic et al. 2006) are plentiful.

Our observation of high biomass of benthivore-piscivores at bulkheads and riprap revetments has implications for the effect of fish on benthos, and vice versa, along hardened shorelines. High biomass of benthivore-piscivores could exert substantial predation pressure on benthic prey. Indeed, decreased or altered prey resources have been reported along hardened shorelines (King et al. 2005; Seitz et al. 2006; Bilkovic et al. 2006; Heerhartz et al. 2015); some species (e.g., juvenile Pacific salmon) have been shown to feed at high rates along both hardened and natural shoreline types (Heerhartz and Toft 2015); and slight negative relationships between predator abundance and benthic infaunal biomass and diversity have been shown in nearshore areas (within 4 m of shore) by at least one study (Lawless and Seitz 2014). Conversely, hardened shorelines could alter prey resources independent of predation pressure, as reported by Lawless and Seitz (2014) for benthic infaunal density. Small fish may also avoid deeper waters created by shoreline armoring (Munsch et al. 2016), given the value of shallow waters as refuge habitat (Ruiz et al. 1993; Hines and Ruiz 1995). Alterations to prey resources could in turn negatively affect fish condition along hardened shorelines. For example, empty stomachs and different prey items found in gulf killifish and spot from hardened wetlands in coastal Mississippi (i.e., wetlands that were fragmented and dominated by hardened surfaces) contributed to lower body condition of those species (Lowe and Peterson 2015). We do not have direct evidence of either mechanism in our study, but based on our biomass findings, we speculate that shoreline hardening will likely affect predator–prey dynamics in nearshore waters.

Differences in biomass responses at extreme nearshore interface areas and broader nearshore zones (defined in our study as waters extending 3 and 16 m from shore, respectively) suggest that biomass patterns may be driven by small-scale distributional shifts related to shoreline characteristics within 3 m from shore. For example, total biomass across all groups was substantially greater at bulkheads than all other types within 3 m from shore, but did not differ among shoreline types within

16 m from shore. Similarly, overall size-specific shoreline utilization was more similar among shoreline types within 16 m from shore than within 3 m from shore, although littoral-demersal species were an exception. We speculate that this difference is driven by greater depth-at-shore at bulkheads, which facilitated access of large-bodied, biomass-rich individuals to waters within 3 m from shore. Similarly, the high biomass of planktivores at riprap and bulkhead shorelines relative to wetland and beach shorelines within 3 m of shore may reflect deeper water and similarity to open-water habitat. Within 16 m of shore, bulkheads held the lowest biomass of planktivores relative to other shoreline types (6.1 vs. ≥ 26.0 g m⁻²). Taken together, this suggests that planktivores at bulkheads were congregated within 3 m of shore. Predation risk in the 3 to 16 m zone may have been higher than in waters extending only 3 m from shore, as the benthivore-piscivore assemblage included larger individuals within 16 m from shore than within 3 m from shore. In addition, planktivorous fish biomass may have been higher along wetland and beach shoreline types within 16 m from shore than in the narrower 3 m ecotone because natural shorelines preserve intertidal areas and planktivores have been shown to feed preferentially on intertidal zooplankton assemblages (David et al. 2016). Some planktivores—specifically, *Menidia* spp. in our study—also rely on wetland shorelines for spawning and nursery habitat (Balouskus & Targett 2012). Finally, littoral-demersal species had high biomass along riprap shorelines relative to wetlands within 3 m from shore (about 47% of the mean biomass observed at wetlands) but not within 16 m from shore (about 13%). This suggests the larger littoral-demersal individuals that utilize riprap habitat do not often venture outside of the relative safety of the riprap itself, while the shallow, turbid, debris-rich waters along wetland shorelines support littoral-demersal species at much greater distances from shore.

Although our study focused on four distinct shoreline types, a number of prior studies have examined changes in fish and invertebrate communities along gradients of partially armored wetlands or beaches (e.g., Bilkovic and Mitchell 2013; Lowe and Peterson 2014; Heerhartz et al. 2015). For example, Lowe and Peterson (2014) described decreasing abundances of three key fish species along a gradient of natural, partially urbanized (i.e., fragmented and hardened), and completely urbanized wetlands, with stronger effects of urbanization on resident species compared to transient species. Several studies have shown living shorelines, which combine wetland plants with a hardened structure, to be more similar to native wetlands than to riprap revetments; living shorelines are therefore considered less harmful than conventional coastal protection methods like bulkhead and riprap and as a result are becoming more widespread (Davis et al. 2008; Currin et al. 2010; Balouskus and Targett 2016; Bilkovic et al. 2016; Gittman et al. 2016b). Greater nekton diversity has also been detected at living shorelines relative to native wetlands,

likely due to the diversity of shoreline habitat (Partyka and Peterson 2008; Peters et al. 2015). Our results suggest living shorelines may have different effects on different functional groups or size classes, meriting additional research.

Taxonomic distinctness and taxonomic variation of assemblages that included both fish and crustaceans indicated natural shoreline types had more diverse assemblages, especially within 3 m from shore, although relationships between taxonomic distinctness, variation and shoreline type were weak overall. Taxonomic distinctness patterns across shoreline type were similar for all species and finfish-only analyses at 3 m from shore, where low taxonomic distinctness at beaches may have reflected a lack of water depth relative to bulkhead and riprap (this study), and less subtidal structure relative to wetlands (Bilkovic and Roggero 2008). Taxonomic distinctness was greater at natural shorelines than hardened shorelines within 16 m of shore for both analyses, but the magnitude of the difference was greater for all species (1.7 units greater on average) than for finfish only (0.8 units greater). This difference is likely driven by the exclusion of grass shrimp, a littoral-demersal species that strongly associates with natural shorelines, from the finfish only analysis. Taxonomic variation was higher for all species along wetland shorelines within 3 m from shore, likely due to the influence of grass shrimp. Importantly, taxonomic variation was still higher along natural shorelines than hardened shorelines within 3 m from shore even for the finfish-only analysis. Average-to-high values of taxonomic diversity combined with high values of taxonomic variation, as observed for natural shorelines within 3 m from shore for all species and finfish, typically indicate more pristine locations (Clarke and Warwick et al. 2001). Furthermore, taxonomic variation measures complexity and low values, as observed for hardened shoreline types in our study within 3 m from shore, may indicate environmental disturbance (Yang et al. 2016). The differences in taxonomic distinctness and variation within 3 m from shore contrast their relative consistency within 16 m from shore, and underscore the other strong effects of hardened shorelines on fauna documented by our study within extreme nearshore interface zones.

Conclusion—Management Considerations

Management applications from our results include considering species-specific or functional-group-specific responses and placing the effects of shoreline hardening into a whole-system context. We provide clear evidence that shoreline types can affect different functional groups in different ways. Although our study focused on the Chesapeake Bay, responses of specific species were generally similar to the response of their respective functional group (Tables 3 and 4). Since the functional groups represented in our study are prevalent in estuaries worldwide, our results may be broadly

applicable to other systems. Based on our findings, it appears that one of the largest effects of shoreline hardening is the alteration of shallow waters at the interface between land and water. These extreme nearshore interface areas, represented in this study by waters within 3 m from shore, tend to be deeper at hardened shorelines than at natural shoreline. Differences in water depth, environmental characteristics, and food availability between natural and hardened shorelines likely contributed to our observed functional group and size-class-specific patterns, and should be considered when making management decisions.

Although this study focused on local-scale effects, system-scale effects may also be important. One major finding of this study is that natural shorelines serve as critically important habitat for resident littoral-demersal species and for juveniles of species from other functional groups. As such, natural shorelines, especially wetlands, are substantially integrated components of larger systems (e.g., Childers et al. 2000; Weinstein et al. 2005), as nursery ground production often moves across habitats and ecosystems (Kneib 1997; Sheaves et al. 2015). Furthermore, whole-system production in coastal estuaries is strongly tied to overall production—including resident species—in intertidal wetlands (Teal 1962; Kneib 1997; Weinstein et al. 2014), and many marine transient species benefit from wetland shorelines and their production without directly occupying those habitats (Litvin and Weinstein 2003; Weinstein et al. 2005). Therefore, shoreline hardening that comes at the expense of wetland habitat likely reduces estuarine production. Given this, it is not surprising that hardened shorelines and wetland loss appear to have cumulative effects on abundance of a variety of fish and crustacean taxa in estuaries (Peterson and Lowe 2009; Dethier et al. 2016; Kornis et al. 2017). Fortunately, high ecosystem productivity, such as when the majority of a subestuary is wetland habitat, can overcome small-scale negative effects of shoreline hardening on infauna, and thus may be important to resilience against shoreline alteration (Lawless and Seitz 2014). We join others (e.g., Weinstein and Litvin 2016) in suggesting a whole-system approach to shoreline management to ensure increased coastal protection needs are met in ways that best maintain healthy estuaries and the ecosystem services they provide.

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