



Acoustic camera and net surveys reveal that nursery enhancement at living shorelines may be restricted to the marsh platform

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ABSTRACT

Rapid human development in coastal areas is introducing significant amounts of novel habitat and leading to widespread habitat simplification. To predict how species will respond to these changes, it is important to understand how organisms interact with novel habitats versus naturally existing habitats. In this study, we used traditional fish sampling gear (fyke nets and minnow traps) and a Dual-Frequency Identification Sonar (DIDSON) to conduct fish surveys along natural and modified estuarine shorelines in North Carolina, USA. The overall objective of our study was to investigate how fish abundance and other community metrics change as a function of shoreline type (natural marsh, living shoreline, or bulkhead), sampling location (marsh platform or the shallow subtidal area offshore of the structure), and time of day (day or night). Using fyke nets, we caught significantly more fish and recorded higher species richness on the marsh platform at living shorelines versus natural marsh shorelines. However, we found no significant differences in fish abundance in the shallow unvegetated habitats seaward of the different shoreline types, which may have been affected by low sampling efficiency and replication when sampled using minnow traps and the DIDSON. Our findings, in conjunction with similar studies, may reflect a localized shoreline effect where the nursery enhancement observed at living shoreline sites is restricted to the living component of the shoreline (i.e., the marsh). Additionally, the preliminary results from our limited daytime versus nighttime DIDSON sampling show no significant differences in fish detections. This contrasts with many previous studies using traditional fish sampling techniques that report substantially higher fish catches at night. This unexpected finding is worthy of additional research as it may suggest that traditional fish sampling techniques are underestimating fish abundances during the day, perhaps due to visual gear avoidance. Ultimately, a careful consideration of the social and ecological goals of any shoreline stabilization project is needed before choosing a final design; however, maximizing habitat restoration and limiting the use of artificial materials is likely to confer the greatest ecological benefit.

1. Introduction

The study of the interaction between species and their structural environment is of fundamental ecological importance (Huffaker, 1958; MacArthur, 1958), particularly in an era of rapid anthropogenic change

and habitat simplification (Hobbs et al., 2013; Cloern et al., 2016). Structural complexity, defined here as the diversity of structural elements (Taniguchi et al., 2003), is thought to be a significant organizing force in marine and terrestrial communities, and it is generally accepted as a primary driver of biodiversity (MacArthur and MacArthur, 1961;

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Murdoch et al., 1972; Menge et al., 1985). Furthermore, increased structural complexity has been shown to enhance the nursery role of habitats for commercially important species (Heck et al., 2003), ameliorate abiotic stressors that are likely to increase with global climate change (Stachowicz, 2001), and modify the interactions between predators and their prey (Savino and Stein, 1982; Heck and Crowder, 1991; Eklöv and Diehl, 1994).

Coastal urbanization and resource exploitation are leading to habitat simplification (i.e., a reduction in structural complexity) in coastal areas across the globe (Hobbs et al., 2013). A common example of habitat simplification is the placement of artificial structures, like seawalls and bulkheads, along shorelines (i.e., shoreline hardening) for the purposes of stabilizing the shoreline or protecting upland infrastructure (United States Army Corps of Engineers, 2016a). Shoreline hardening often results in the replacement of a complex shallow-water habitat (e.g., salt-marsh, mangrove, rocky intertidal) with a more homogenous structure (e.g., smooth vertical seawall) (Bulleri and Chapman, 2010). This reduction in shoreline complexity has been associated with decreased biodiversity (Bilkovic and Roggero, 2008; Gittman et al., 2016b; Kornis et al., 2018) and altered community dynamics such as species interactions and prey selection (Jackson et al., 2008; Munsch et al., 2017).

In response to widespread shoreline hardening, there has been a growing desire to incorporate habitat restoration into shoreline protection schemes to enhance social and ecological resilience and to maintain critical ecosystem services (Dafforn et al., 2015a; Sutton-Grier et al., 2015). The result has been the promotion of natural or nature-based infrastructure that includes the conservation or restoration of natural ecosystems with or without added structural components (Dafforn et al., 2015b; Smith et al., 2020). A common nature-based infrastructure design used in the United States includes an offshore breakwater or restored oyster reef (made from granite rocks, marl, or bagged/loose oyster shell) in combination with existing or planted marsh grasses landward of the breakwater (hereon referred to as a living shoreline; (United States Army Corps of Engineers, 2016b). Living shorelines can maintain the coastal ecosystem services provided by saltmarshes and oyster reefs, while also providing increased protection from erosion due to wave action, storm events, and boat wakes (Manis et al., 2015; Smith et al., 2018; Chowdhury et al., 2019). Furthermore, living shorelines preserve or enhance natural habitat heterogeneity via the intertidal breakwater that replaces soft bottom where structure was previously limited, and increasing the heterogeneity of marine infrastructure has been shown to enhance biodiversity (Strain et al., 2018). However, unvegetated soft bottom is an important habitat in and of itself, and the merits of replacing soft-bottom with an artificial breakwater or restored oyster reef is a topic of debate (Bilkovic and Mitchell, 2013). Nevertheless, the combination of different structural habitat elements within a living shoreline may expand the functional role that living shorelines can play in the coastal environment (Erdle et al., 2006).

In contrast to the widely reported detrimental effects of hardened shorelines, recent studies have shown that fish abundances are maintained and in some cases even enhanced along living shorelines as compared to natural shorelines (Currin et al., 2008a; Scyphers et al., 2011; Balouskus and Targett, 2016; Gittman et al., 2016a). This may be a function of the increased structural complexity associated with the breakwater (Jennings et al., 1999) that acts to attract or produce fish by providing increased access to refuge, prey, or substrate. Despite these findings, fish use of the oyster reef and breakwater structures have rarely been sampled and little is known about the mechanism(s) driving the higher observed abundances.

Estuarine fish living in complex intertidal habitats are notoriously hard to sample (Rozas and Minello, 1997), particularly when comparing across habitats of different complexities or across different light regimes. In the last two decades, use of underwater video for fish sampling has become more prevalent thanks to improved technology, better access to such technology, and potential advantages over traditional methods (e.g., nets, seines, trawls, diver surveys, etc.), specifically that videos are

non-extractive, non-invasive, and easy to replicate (Mallet and Pelletier, 2014). However, one notable limitation of traditional video footage (e.g., GoPro's) is that turbidity in shallow subtidal estuarine habitats is typically high, which inhibits the detection of fish under certain conditions. Few techniques exist which can be used to sample the fish community equally regardless of structure, light limitations, or turbidity.

In this study, we used traditional fish sampling gear (i.e., fyke nets and minnow traps) in addition to a Dual-frequency Identification Sonar (DIDSON; Sound Metrics Corporation, Bellevue, WA) to determine whether shoreline type in a shallow suburban estuary has an effect on fish abundance and other community metrics. DIDSONs are portable "acoustic cameras" that can collect video quality images in shallow water settings (Becker et al., 2011; Martignac et al., 2015), but they use sound instead of light to image, and thus are not limited by light availability or turbidity. Based on previous research, we hypothesized in this study that: i) fish abundance, biomass, and species richness would be highest at living shoreline sites and lowest at bulkheads (Scyphers et al., 2011; Gittman et al., 2016a); and, ii) the abundance of fish across all shorelines would be higher at night than during the day (Rountree and Able, 1993; Beauchamp et al., 1994; Guest et al., 2003; Erika Young, 2017). Furthermore, we were interested in using the DIDSON to investigate some of the potential mechanisms underlying the fish enhancement that has been observed in other living shoreline studies. Past studies have speculated that higher fish abundances at living shoreline and natural shoreline sites could be a function of the increase in structural complexity or multiple habitat components (Erdle et al., 2006) providing greater spatial refuge or superior access to food via the colonization of the sill with epibionts and epifauna (Gittman et al., 2016a). Thus, we also hypothesized that: iii) structural affinity (i.e., association between fish and the structure, using distance as a proxy) would be strongest along shorelines that were more complex (i.e., living shorelines) and weakest along shorelines that were more homogenous (i.e., bulkheads); and, iv) structural affinity would be stronger during daylight hours when prey are more vulnerable to visual detection by predators.

2. Methods

2.1. Site descriptions

To investigate fish use of natural and modified estuarine shorelines, we conducted two independent studies in the summers of 2016 and 2017 in eastern North Carolina. The first study (hereafter referred to as fyke net sampling) used fyke nets to measure fish use of the marsh platform at natural reference marsh sites (Fig. 1A) and paired living shorelines (Fig. 1B). The sites were grouped in four geographic regions, each with one living shoreline and one reference marsh: Hatteras (35°13'18.8"N 75°41'35.9"W), Bogue Banks (BB; 34°42'12.4"N 76°48'21.0"W), Jones Island (JI; 34°41'52.1"N 77°06'26.7"W), and Morris Landing (ML; 34°28'11.4"N 77°30'28.3"W) (Fig. 2). All living shoreline sites were composed of an offshore sill (i.e., breakwater) made from either granite rocks or bagged oyster shell and planted with *Spartina alterniflora* marsh grass landward of the sill (Table 1). The sill at JI was largely buried under new sediment, but the oysters that had recruited to the sill were still apparent along the shoreline. All reference marshes were dominated by *S. alterniflora* and located within 500 m of the living shoreline sites (Table 1). Fyke nets were set to sample the marsh platform (i.e., the area landward of the sill) and were placed at dropdowns or gaps in the sill (Fig. 3).

The second study (hereafter referred to as DIDSON sampling) was conducted in the summer of 2017 at nine sites in Carteret County, NC and included sampling with the DIDSON and minnow traps. Sites were geographically grouped within the following three regions: Duke University Marine Lab (Duke; 34°43'07.8"N 76°40'23.2"W); Pine Knoll Shores (PKS; 34°42'12.4"N 76°48'21.0"W); and the Pine Knoll Shores

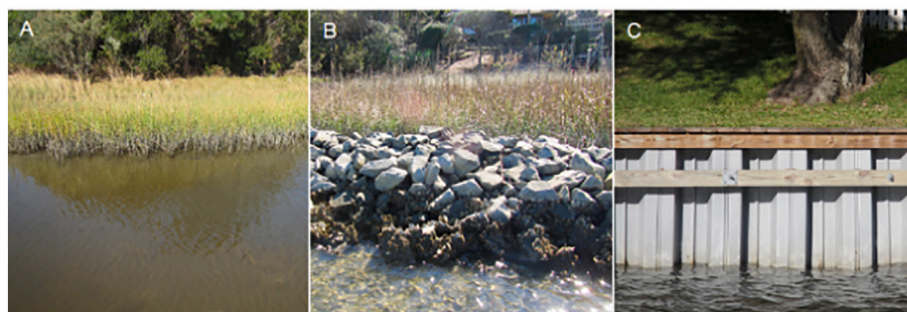


Fig. 1. The shoreline types sampled in this study include: (A) fringing *Spartina alterniflora* saltmarsh, (B) rock sill living shoreline with an offshore granite breakwater, and (C) corrugated sheet pile bulkhead. Photos were taken near low tide.

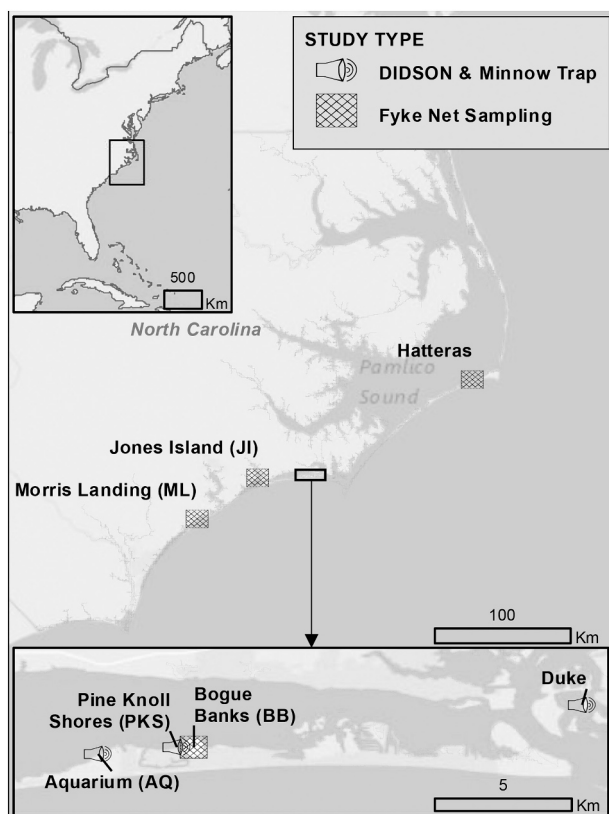


Fig. 2. Map showing the geographic distribution of fyke net sampling sites and DIDSON and minnow trap sampling sites in coastal North Carolina.

Aquarium (AQ; 34°42'04.2"N 76°49'54.6"W)(Fig. 2). Each region contained one natural marsh, one living shoreline, and one bulkhead (Fig. 1). The living shoreline sampled in PKS was the same as the living shoreline sampled in BB in the Fyke Net Study, but all other sites were unique. All living shorelines had a granite breakwater and were planted with *S. alterniflora*. Construction dates for bulkheads are unknown, but all are composed of vinyl sheet pile (Table 1). The corrugation interval on the PKS and AQ bulkheads is approximately 0.25 m, whereas the corrugation interval at the Duke bulkhead is approximately 0.5 m. Natural reference marshes are all narrow fringing marshes (< 10 m) dominated by *S. alterniflora*. All DIDSON and minnow trap sampling at living shoreline sites was conducted along the outside edge of the sill (i. e., seaward side), and away from dropdowns and overlaps (Fig. 3). Across all regions, bulkheads were deeper at the structure edge than living shorelines, and natural marsh shorelines were the shallowest (Table 1).

2.2. Fyke net sampling

Fyke net sampling was conducted monthly from June–September 2016, for a total of four sampling events at each site. At each paired living shoreline and marsh site, two fyke nets per site were simultaneously placed in the water along the vegetated edge of the natural marsh (i.e., facing the marsh) or along the inside edge of the sill facing the marsh (i.e., on the inside of the sill through dropdowns or gaps). The fyke nets had a 1 m × 1 m × 5 m central mesh bag (3 mm mesh), with wings (1 m × 5 m) extending from either side. Sampling was conducted during spring tides for maximum tidal difference. Nets were set at nighttime high tide and retrieved approximately six hours later at low tide. All fish caught were identified to the lowest taxonomic level possible (typically species), counted, and weighed wet. Data were pooled across the two nets at each site and fish abundance and biomass are reported as Catch Per Unit Effort (CPUE; i.e., fish per 2 nets per 6 h soak).

2.3. DIDSON sampling

We sampled all sites every two weeks with the DIDSON during the day from June through July 2017, and additionally sampled each site once at night in July for a total of six sampling events. It is worth emphasizing here that the day/night comparison had only one temporal replicate and thus these data should be interpreted as preliminary. We used the high-frequency (1.8 Hz) mode on the DIDSON, which is best for collecting high-resolution imagery at short distances (< 12 m). Furthermore, we used a specialized 8-degree concentrator lens (Ocean Marine Industries) to reduce refraction from the water surface and optimize the view field in shallow water. The DIDSON was mounted on an aluminum frame and deployed 5 m from the edge of each shoreline facing towards the shoreline (Fig. 3; see Supplementary Fig. 1 for an example of DIDSON imagery). We used the real-time viewing in DIDSON software to confirm the correct distance and orientation. The DIDSON sampling required a water depth of approximately 0.5 m, so we limited our sampling window to the two hours around high tide. For each sampling event, we sampled for a total of 10 min, including a 5-min acclimation period after the DIDSON was placed (which is considered an appropriate amount of time for fish to return after a disturbance; Graham, 1992), followed by 5 min of footage that were used for analysis (with an approximate frame rate of eight frames per second). For the day/night sampling, each site was sampled during the day and at night within the same 24-h period.

Identification of fish species in our study system using DIDSON alone is difficult or impossible unless the species of interest is morphologically distinct. To address this, we also set replicate unbaited minnow traps ($n = 5$) along the outside edge of each shoreline. Minnow trap sampling was conducted within 24 h of daytime DIDSON sampling (but not simultaneously, so as not to interfere with the viewing window) during four of the sampling dates at each site. Minnow traps were primarily

Table 1Description of study sites. Mean depths show mean \pm SE with n in parentheses. Under treatment, LS = living shoreline and BH = bulkhead.

Fyke Net Study						
Region	Treatment	Material Type	Year built	Tidal amplitude	Mean depth of net at deploy (cm)	Mean depth of net at retrieval (cm)
Hatteras	Marsh			< 0.5 m	32 \pm 5 (4)	23 \pm 3 (4)
Hatteras	LS	Granite	2011	< 0.5 m	41 \pm 4 (4)	34 \pm 3 (4)
BB	Marsh			0.5–1 m	81 \pm 6 (4)	16 \pm 1 (4)
BB	LS	Granite	2012	0.5–1 m	61 \pm 8 (4)	8 \pm 3 (4)
JI	Marsh			0.5–1 m	86 \pm 5 (4)	46 \pm 3 (4)
JI	LS	Bagged oyster shell	2010	0.5–1 m	81 \pm 6 (4)	44 \pm 5 (4)
ML	Marsh			> 1 m	58 \pm 3 (4)	32 \pm 5 (4)
ML	LS	Bagged oyster shell	2011	> 1 m	72 \pm 3 (4)	43 \pm 6 (4)
DIDSON Study					Mean depth at structure edge (cm)	Mean depth at DIDSON frame (cm)
Duke	Marsh			0.5–1 m	43 \pm 2 (2)	62 \pm 1 (2)
Duke	LS	Granite	2002	0.5–1 m	66 \pm 6 (2)	105 \pm 4 (2)
Duke	BH	Vinyl	After 2002	0.5–1 m	90 \pm 11 (2)	105 \pm 12 (2)
PKS	Marsh			0.5–1 m	39 \pm 16 (2)	69 \pm 16 (2)
PKS	LS	Granite	2012	0.5–1 m	53 \pm 13 (2)	64 \pm 12 (2)
PKS	BH	Vinyl	Unknown	0.5–1 m	61 \pm 14 (2)	68 \pm 12 (2)
AQ	Marsh			0.5–1 m	32 \pm 17 (2)	62 \pm 15 (2)
AQ	LS	Granite	2002	0.5–1 m	51 \pm 18 (2)	74 \pm 10 (2)
AQ	BH	Vinyl	Unknown	0.5–1 m	89 \pm 14 (2)	97 \pm 16 (2)

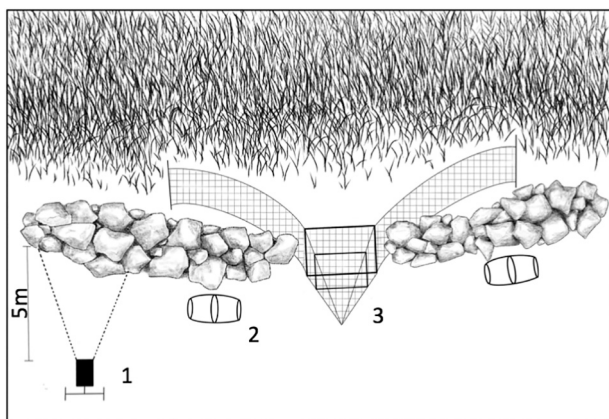


Fig. 3. Sampling schematic showing the approximate areas sampled by each gear along a living shoreline with a fringing marsh and granite sill. The numbers denote the positioning of: (1) the DIDSON (5 m offshore of the structure), (2) minnow traps (against the outside edge of the structure), and (3) fyke nets placed at dropdowns/gaps in the sills.

indexing the small fish species, as the largest fish we caught in our traps was 8.5 cm, therefore minnow trap catches are likely not representative of the full fish community observed with the DIDSON. Traps were set two hours before high tide and pulled two hours after high tide, for a total soak time of four hours. Sites within a region (i.e., one marsh, one living shoreline, one bulkhead) were sampled simultaneously. Fish were identified to species, counted, and weighed wet. We pooled across all five traps at each site on each date and fish abundance and biomass are reported as CPUE (fish per 5 traps per 4 h soak). At one site, on one occasion, we only recovered four of the five minnow traps, so the counts and biomass for that trap were multiplied by a factor of 5/4, and the total count was rounded to the nearest whole number for analysis.

2.4. Video analysis

DIDSON footage was manually processed for fish counts and sizes within the DIDSON software package (Version 5.26.06; Sound Metrics Corp.). All fish count data is presented as meanN, which is calculated by averaging the total fish counts per subsample (i.e. different frames from within a single video), to get one mean count value per video. MeanN is more robust for subsample analysis than the commonly used maxN (which uses the single subsample with the highest count of fish) because

it is less susceptible to bias associated with large fish schools and it has been shown to be more strongly related to true abundance than maxN (Schobernd et al., 2014). Mean count also allows for statistical summaries of fish length measurements that would otherwise be limited to a single frame that may contain only a single species or size class of fish.

To identify the optimal number of subsamples per 5-min video to use for analysis, we selected 50 frames as a baseline. Using a custom function in R (RStudio Team, 2016), we randomly selected 50 frames from each 5-min video (comprised of approximately 2500 individual frames) that were separated by at least 25 frames so that the subsamples were stratified across the entire video. For each frame subsample, we used the 5 frames on either side of the selected frame to detect movement of fish or to find the optimal fish orientation for length measurement. We then recorded the total number of fish per subsample, the length of each fish, and the distance between each fish and the DIDSON transducer. To determine the optimal number of subsamples, we analyzed the data pulled from the first eight randomly selected videos by running 1000 bootstrap simulations to calculate meanN for all frame sample sizes between 5 and 50 (at an interval of 5 frames). We then visually inspected the variance in meanN across all sample sizes and determined that 25 subsamples maintained sufficient precision and a coefficient of variation below 0.20 for all but one of the eight videos (Supplementary Table 1; Supplementary Fig. 2). Accordingly, the remaining videos were processed by randomly selecting 25 frame subsamples from each video (separated by at least 50 frames). When it came time to analyze the data for the first eight videos that had 50 subsamples, we randomly selected one out of every two frames to include in our statistical analyses.

The majority of fish in the videos were individually measured, but when there were larger schools of fish or when individuals were hard to distinguish, we estimated the total number of fish in the school, the average size of the fish, and average distance to transducer and used that to estimate the total number of fish, fish size, and fish distance. We excluded all fish that were within 2 m of the DIDSON transducer to account for any aggregating effect of the DIDSON frame itself. Additionally, we excluded all fish smaller than 4 cm because they could not be reliably detected (Able et al., 2014). Finally, we measured the position of the structure edge at bulkhead and living shoreline sites to account for any small differences in DIDSON placement and used the position of the structure edge to calculate fish structural affinity (described below). To remain consistent, a single skilled reviewer conducted all DIDSON image processing.

DIDSON data were analyzed separately as daytime fish counts (aggregate of all daytime videos) and day/night fish counts (only the nighttime videos and daytime videos that were taken within 24 h of the

nighttime videos). To calculate fish structural affinity, we used distance between the fish and the structure edge as a proxy. This comparison was only conducted at bulkhead and living shoreline sites because the edge of natural marsh shorelines was not easily defined. Distance was calculated by measuring the distance between the DIDSON transducer and the structure edge and then subtracting the distance between each fish and the transducer (note that it was possible to have negative distance numbers if the fish were observed past the edge of the structure).

2.5. Statistical analysis

To analyze the fyke net data, we first used Generalized Linear Mixed Effects Models (GLMMs; Bolker et al., 2009) to model fish abundance and fish species richness. For each model, treatment (categorical with two levels: marsh and living shoreline) and region (categorical with four levels: Hatteras, BB, JI, ML) were included as fixed effects, and a grouping factor that controlled for repeated measurements over time at the same sites was included as a random effect (i.e., Site ID; 8 levels). The models were fit using the ‘glmmTMB’ package (Brooks et al., 2017). We compared model fit using AIC among Poisson, Generalized Poisson, and negative binomial distributions to find the best fit for the data. Once we selected the final distribution, we used Likelihood Ratio Tests (LRTs) to assess the associations between the response variables and predictor variables (treatment and region) for each model. To model fish biomass, which was a continuous response rather than discrete as above, we used Linear Mixed Effects Models (LMMs) using Restricted Maximum Likelihood (REML) in the ‘nlme’ package (Pinheiro et al., 2020). As above, we included treatment and region as fixed effects, and a grouping factor to account for repeated measurements as a random effect. We visually examined model residuals to determine whether the data met test assumptions, and we performed square root or log transformations when necessary. We did not include an interaction term in these models (i.e., Treatment*region) as we had no *a priori* reason to believe that the treatment effect would be conditionally dependent on region and we did not want to overfit the models.

Similarly, we used GLMMs to analyze minnow trap fish catches and fish species richness, and we used LMMs to analyze minnow trap fish biomass. For all models, we included treatment (categorical with three levels: marsh, living shoreline, bulkhead) and region (categorical with three levels: AQ, PKS, and Duke) as fixed effects with no interaction (see above) and a grouping factor that controlled for repeated measurements over time at the same sites as a random effect (i.e., Site ID; 9 levels).

We also used LMMs to analyze daytime DIDSON meanN metrics and to compare average fish distance to the structure edge with the same factors above, except that the distance test only had two treatment levels (i.e., bulkhead and living shoreline). We used LMMs, not GLMMs as for the fyke net data, to analyze all the DIDSON data as the response variables were not true counts (they were average counts). To compare fish size distributions across shoreline types for the daytime DIDSON data, we pooled all length measurements by treatment and used two-sided bootstrapped Kolmogorov-Smirnov (KS) tests from the ‘Matching’ package in R (Sekhon, 2011). We conducted pairwise comparisons between each of the shoreline types with 1000 Monte Carlo simulations for each test (*sensu* Kornis et al., 2018).

For the day/night DIDSON samples, we used two-way ANOVA with treatment (categorical with three levels: marsh, living shoreline, and bulkhead), time of day (categorical with two levels: day and night), and the interaction between treatment and time of day as fixed effects to analyze meanN and to compare average fish distance to the structure edge (the distance test only had two treatment levels: bulkhead and living shoreline). We included an interaction term in this model because it was ecologically relevant to our hypothesis that light gradient might interact with structure type. Before running the two-way ANOVA, we first ran LMMs to account for the non-independence of observations at the same sites (which were sampled once during the day and once at night), but the models would not converge to produce a *p*-value as the

replication in our preliminary day/night comparison was insufficient for a random effects model. Thus, the final ANOVA models are less conservative than the LMMs and results should be interpreted with this in mind. To compare fish size distribution by time of day, we pooled all fish length measurements by time of day and used a KS test as above to compare size distributions between day and night. All statistical analyses were conducted in R Version 4.0.2 (RStudio Team, 2016), and we used an alpha level of 0.05.

3. Results

3.1. Fyke net sampling

Across all regions and dates with the fyke net sampling we caught 23 species of fish at living shoreline sites and 22 species of fish at marsh sites. Pinfish (*Lagodon rhomboids*) were by far the most abundant fish species caught along both living shorelines and marsh shorelines, followed by mullet (*Mugil* spp.) and silversides (*Menidia* spp.) (Table 2). Overall, fish abundances were significantly higher at living shorelines versus reference marshes (GLMM; $\chi^2 = 10.04$, $p = 0.002$) and significantly different among regions ($\chi^2 = 15.84$, $p = 0.001$) (Fig. 4A). Fish biomass was not significantly different between treatments (LMM; $F = 5.63$, $p = 0.10$) or regions (LMM; $F = 2.18$, $p = 0.27$) (Fig. 4B). Species richness was significantly higher at living shoreline sites versus reference marsh sites (GLMM; $\chi^2 = 10.58$, $p = 0.001$) and also significantly different among regions ($\chi^2 = 8.02$, $p = 0.046$) (Fig. 4C; Supplementary Tables 2 & 3; Supplementary Fig. 3).

3.2. Minnow trap sampling

For the minnow trap sampling, across all sampling dates and sites we caught five species of fish along natural shorelines (Mummichog [*Fundulus heteroclitus*], naked goby [*Gobiosoma bosc*], pinfish, oyster toadfish [*Opsanus tau*], and pigfish [*Orthopristis chrysoptera*]), three species along living shorelines (mummichog, pinfish, and pigfish), and only two species of fish along bulkhead shorelines (pinfish and pigfish; Table 3). More individuals were caught along natural shorelines as compared to living shorelines and bulkhead shorelines, but these differences were not statistically significant by treatment (GLMM; $\chi^2 = 5.50$, $p = 0.06$) or region ($\chi^2 = 2.50$, $p = 0.29$) (Fig. 5A). Total fish biomass was not significantly different by treatment (LMM; $F = 0.39$, $p = 0.70$) or region ($F = 0.35$, $p = 0.72$) (Fig. 5B). There were no differences in fish species richness among shoreline types (GLMM; $\chi^2 = 1.5$, $p = 0.47$) or regions ($\chi^2 = 0.25$, $p = 0.89$) (Fig. 5C; Supplementary Tables 2 & 3; Supplementary Fig. 4).

3.3. DIDSON daytime sampling

Across all daytime videos and sampling dates we recorded 1590 fish in front of bulkhead shorelines, 1531 fish in front of marsh shorelines, and 1125 fish in front of living shorelines. The vast majority of fish detected with the DIDSON were small (< 20 cm); only 39 fish were longer than 20 cm and the longest individual was 71 cm (Fig. 6A). The cumulative length distribution of all fish pooled along bulkhead shorelines was significantly different than along living shorelines (KS test; $p < 0.001$) and natural marsh shorelines ($p < 0.001$). Length distributions were not statistically different between natural marsh and living shorelines ($p = 0.22$) (Fig. 6B). Fish counts were not statistically different among treatments (LMM; $F = 1.08$, $p = 0.42$), but there was a marginally significant difference among regions ($F = 6.67$, $p = 0.05$) (Fig. 6C). There was no significant difference in structural affinity of fish between bulkheads and living shorelines ($F = 0.66$, $p = 0.50$) or between regions ($F = 3.44$, $p = 0.23$) (Fig. 6D; Supplementary Table 3; Supplementary Fig. 5).

Table 2Fyke net species list. Catches and biomass are reported as means with SE in parentheses ($n = 4$ regions).

Species	Common Name	Living Shoreline		Marsh	
		Ind/6 h	Biomass (g/6 h)	Ind/6 h	Biomass (g/6 h)
Fish					
<i>Lagodon rhomboides</i>	Pinfish	47.2 (24.1)	392.4 (200.1)	25.2 (15.0)	122.5 (52.7)
<i>Mugil spp.</i>	Mullet	14.7 (7.7)	60.7 (16.3)	3.4 (1.3)	40.7 (32.5)
<i>Menidia spp.</i>	Silverside	12.8 (3.8)	77.7 (19.1)	3.4 (1.2)	6.6 (2.9)
<i>Brevoortia smithi</i>	Yellowfin menhaden	10.7 (5.2)	19.6 (8.1)	0.8 (0.3)	14.2 (13.1)
<i>Leiostomus xanthurus</i>	Spot	7.9 (3.4)	33.5 (14.5)	1.6 (1.1)	7.6 (5.7)
<i>Orthopristis chrysoptera</i>	Pigfish	2.4 (0.4)	22.7 (5.7)	1.5 (0.9)	8.2 (3.6)
<i>Eucinostomus spp.</i>	Mojarra	1.3 (0.8)	2.9 (1.5)	0.5 (0.4)	2.1 (1.6)
<i>Fundulus majalis</i>	Striped killifish	1.3 (0.7)	10.5 (10.1)	0.1 (0.1)	0.1 (0.1)
<i>Paralichthys spp.</i>	Flounder	1.3 (0.5)	127.5 (49.6)	0.3 (0.2)	13.8 (9.7)
<i>Micropogonias undulatus</i>	Atlantic croaker	1.2 (0.5)	5.9 (2.3)	0.6 (0.2)	1.3 (0.9)
<i>Bairdiella chrysoura</i>	Silver perch	0.7 (0.4)	10.2 (5.2)	0.2 (0.1)	3.0 (2.4)
<i>Fundulus heteroclitus</i>	Mummichog	0.6 (0.3)	2.4 (1.3)	0.3 (0.1)	0.9 (0.7)
<i>Synodus foetens</i>	Inshore lizardfish	0.3 (0.3)	3.1 (3.1)	0.0 (0.0)	0.0 (0.0)
<i>Trachinotus falcatus</i>	Permit	0.2 (0.1)	0.42(0.2)	0.1 (0.1)	0.1 (0.1)
<i>Gobiosoma spp.</i>	Goby	0.1 (0.1)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Sciaenops ocellatus</i>	Red drum	0.1 (0.1)	108.8 (105.4)	0.1 (0.1)	78.1 (78.1)
<i>Strongylura marina</i>	Atlantic needlefish	0.1 (0.1)	3.6 (2.7)	0.0 (0.0)	0.0 (0.0)
<i>Symphurus plagiusa</i>	Blackcheek tonguefish	0.1 (0.1)	0.0 (0.0)	0.2 (0.1)	0.5 (0.4)
<i>Anchoa mitchilli</i>	Bay anchovy	0.1 (0.1)	0.0 (0.0)	0.8 (0.5)	1.1 (0.9)
<i>Cynoscion nebulosus</i>	Speckled trout	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	5.0 (5.0)
<i>Gobiesox strumosus</i>	Skilletfish	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Hemiramphus brasiliensis</i>	Ballyhoo	0.1 (0.1)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)
<i>Opsanus tau</i>	Oyster toadfish	0.1 (0.1)	6.1 (6.1)	0.0 (0.0)	0.0 (0.0)
<i>Stephanolepis setifer</i>	Pigmy filefish	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.1 (0.1)
<i>Archosargus probatocephalus</i>	Sheepshead	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
<i>Cyprinodon variegatus</i>	Sheepshead minnow	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)
<i>Histrio histrio</i>	Sargassumfish	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.3 (0.3)
<i>Morone americana</i>	White perch	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.4 (0.4)

3.4. DIDSON day/night sampling

Across all day/night videos we recorded 713 fish during the day and 596 fish during the night. The vast majority of fish detected with the DIDSON were small (< 20 cm); only 57 fish were longer than 20 cm and the longest individual was 49 cm (Fig. 7A). The cumulative length distribution of all fish pooled was significantly different between day and night samples (KS test; $p = 0.02$) with a higher probability of detecting small fish at night (Fig. 7B). There were no statistical differences in DIDSON fish detections by shoreline type (Two-way ANOVA; $F_{2,12} = 1.10$, $p = 0.36$), time of day ($F_{1,12} = 0.40$, $p = 0.54$) or the interaction between the two ($F_{2,12} = 2.06$, $p = 0.17$) (Fig. 7C). There were no significant differences in structural affinity of fish between treatment ($F_{1,8} = 4.27$, $p = 0.07$), time of day ($F_{1,8} = 0.07$, $p = 0.80$), or the interaction between the two ($F_{1,8} = 0.38$, $p = 0.56$) (Fig. 7D; Supplementary Table 4).

4. Discussion

Our surveys of the marsh platform behind the sill at living shoreline sites showed higher fish abundances and higher fish species richness than natural reference marshes, supporting our main hypothesis. However, our surveys of the shallow subtidal area seaward of marsh, living shoreline, and bulkhead sites did not show any significant differences among shoreline types, though the minnow trap and DIDSON surveys had more limited temporal replication than the fyke net sampling. Our results, in conjunction with similar studies, suggest that the nursery enhancement observed at living shoreline sites may be restricted to the marsh platform behind the living shoreline breakwater rather than the structural component of the breakwater itself.

Previous sampling of the fish community at living shoreline sites versus natural reference marshes has typically been designed to sample either: 1) the unvegetated area seaward of the shoreline (Balouskus and Targett, 2016); or, 2) use of the marsh platform or area behind the living shoreline breakwater (Currin et al., 2008a; Scyphers et al., 2011). In one

study that sampled both the unvegetated area landward of the shoreline and use of the marsh platform, the findings differed between the two sampling designs (Gittman et al., 2016a). In that study, sampling of the marsh platform with fyke nets revealed significantly higher fish abundances and fish diversity along living shorelines than natural shorelines. Similarly, our fyke net catches from the marsh platform behind living shorelines showed higher fish catches and species richness, which provides further support for the hypothesis that installing a living shoreline can enhance the nursery value of eroding marsh shorelines. In contrast, when Gittman et al. (2016a) used seine nets to sample the unvegetated area seaward of the shoreline at the same sites as above, they found no significant differences in the fish community among shoreline types. It is worth noting here that catch is a reflection of both abundance and catchability, and it is possible that higher catches are due to the selectivity of different gear types or the catchability of fish in different environments, rather than a true reflection of their abundance (Bacheler and Shertzer, 2020).

Contrary to the fyke net data, our minnow trap sampling at living shoreline, bulkhead, and natural marsh sites did not find any significant differences in fish catches or biomass. It is notable that Gittman et al. (2016a) also used minnow traps to sample marsh, living shoreline, and bulkhead sites in NC and caught significantly more fish at living shoreline sites than bulkhead sites. We attribute this inconsistency between our studies to the fact that: 1) Gittman et al. (2016a) used ten minnow traps per site (versus our five) and thus had more statistical power for detecting differences; and, 2) minnow traps in that study were set behind the sill, rather than in front of the sill as in our study. Minnow traps behind the breakwater are presumably sampling both fish use of the breakwater itself and fish use of the refuge and marsh behind the breakwater, whereas our minnow traps on the outside of the breakwater were testing fish use of the structural component of the breakwater alone. In contrast, Balouskus and Targett (2016) used minnow traps to sample the seaward edge of marshes, living shorelines, and revetments, and similar to our results they did not find enhanced fish abundances or species richness in front of living shorelines. Exclusively sampling along

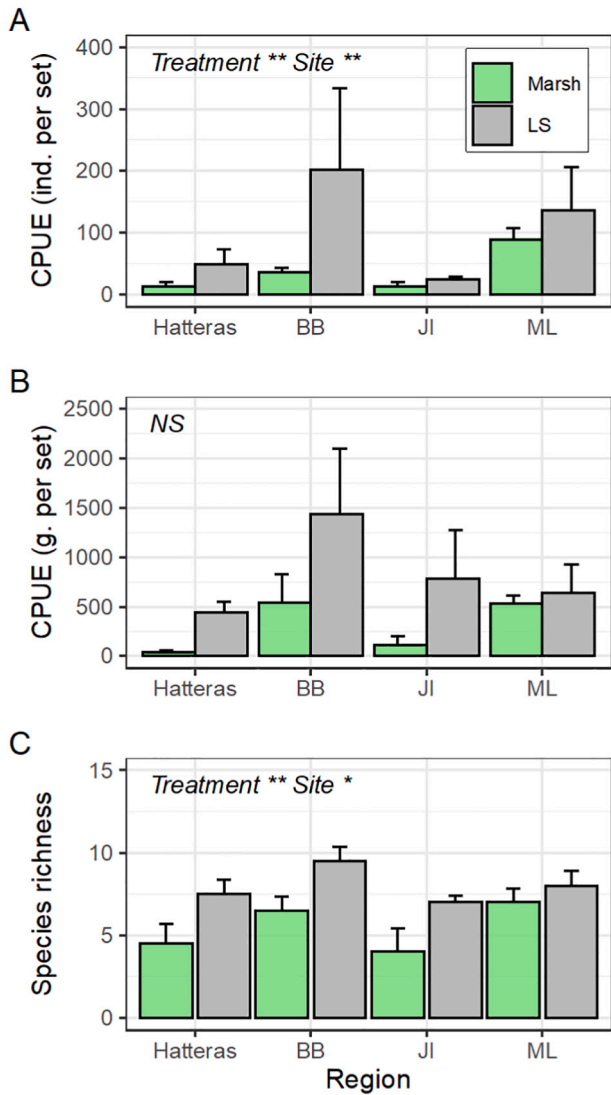


Fig. 4. Fyke net Catch Per Unit Effort (CPUE) by shoreline type for (A) individuals caught, (B) total biomass, and (C) fish species richness. Bars show mean \pm SE (n = 4 sampling dates). LS = living shoreline and Marsh = natural reference marsh.

Table 3

Minnow Trap species list. Catches and biomass are reported as means with SE in parentheses (n = 3 regions).

Species (Common name)	Living Shoreline		Marsh		Bulkhead	
	Ind/6 h	Biomass (g/6 h)	Ind/6 h	Biomass (g/6 h)	Ind/6 h	Biomass (g/6 h)
Fish						
<i>Lagodon rhomboides</i> (Pinfish)	0.8 (0.4)	2.4 (1.2)	0.7 (0.4)	2.3 (1.2)	1.3 (0.6)	5.3 (2.6)
<i>Fundulus heteroclitus</i> (Mummichog)	0.2 (0.2)	1.3 (1.3)	6.2 (6.0)	20.5 (19.6)	0.0 (0.0)	0.0 (0.0)
<i>Orthopristis chrysoptera</i> (Pigfish)	0.2 (0.2)	0.5 (0.5)	0.3 (0.1)	0.6 (0.2)	0.3 (0.1)	0.7 (0.0)
<i>Gobiosoma bosc</i> (Naked goby)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
<i>Opsanus tau</i> (Oyster toadfish)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)

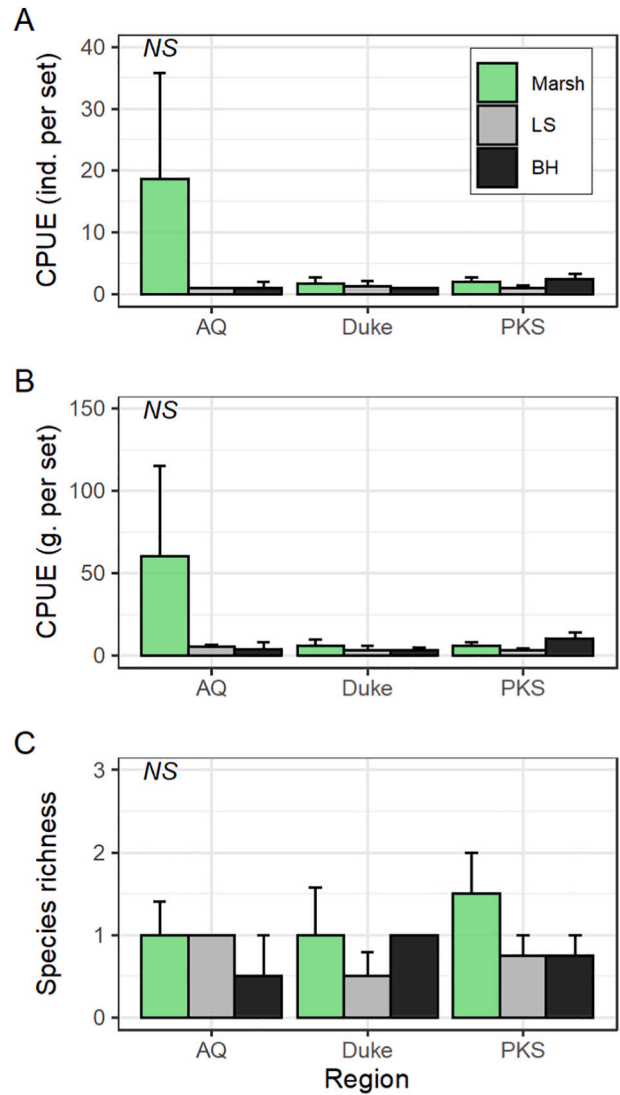


Fig. 5. Minnow trap Catch Per Unit Effort (CPUE) by shoreline type for (A) individuals caught, (B) total biomass, and (C) fish species richness. Bars show mean \pm SE (n = 4 sampling dates). LS = living shoreline, BH = bulkhead, and Marsh = natural reference marsh.

the outside of the breakwater may produce results that are comparable to sampling along a revetment (i.e., a sloping rock shoreline where there is no marsh behind the structure), and while revetments are often ecologically preferable to bulkheads they still typically host fewer organisms than natural shorelines (Erdle et al., 2006; Seitz et al., 2006; Bilkovic and Roggero, 2008).

Similar to the results from the minnow trap sampling, DIDSON sampling did not show any significant differences in fish abundance by shoreline type; however, there were statistical differences in the size frequency distribution of fish between bulkheads and the other two shoreline types. The cumulative length distribution of fish at living shorelines and natural shorelines were more similar than along bulkhead shorelines, where fish tended to be slightly larger; this, in addition to our fyke net sampling, offers further support that living shorelines are providing more suitable habitat for small fish. Kornis et al. (2018) found similar results when sampling the shallow subtidal area seaward of natural, bulkhead, and revetment shorelines in the Chesapeake Bay. The authors found that fish tended to be larger along bulkhead and revetment shorelines than along natural shorelines. The fact that living shorelines and marshes had similar size frequency distributions in our study may be a reflection of water depth. Our natural marsh sites were

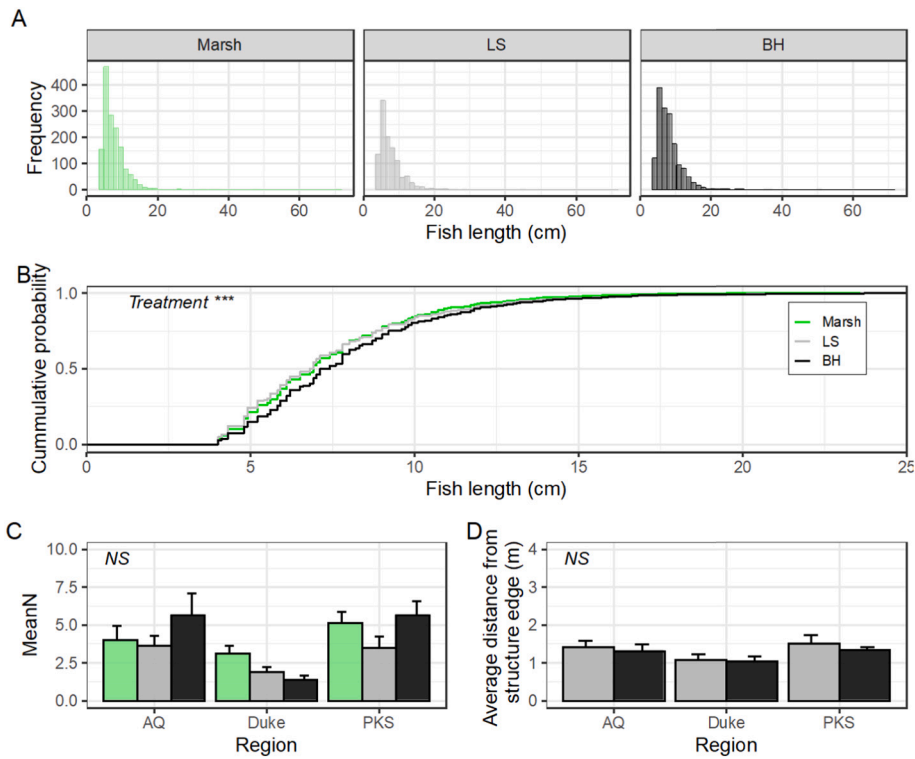


Fig. 6. Metrics from daytime DIDSON fish sampling. (A) Shows the size frequency distribution of all fish across shoreline types and all sampling dates. (B) Shows the cumulative size frequency distribution curves for different shoreline types; the x-axis has been truncated to highlight the differences between treatments (19 length records are not shown as they exceeded 25 cm). (C) Shows the average number of fish detections (meanN) by shoreline type and region. (D) Shows the average distance between fish and the structure edge along living shoreline and bulkheads shorelines. Bars show mean \pm SE (n = 5 sampling dates). M = natural reference marsh, LS = living shoreline, and BH = bulkhead.

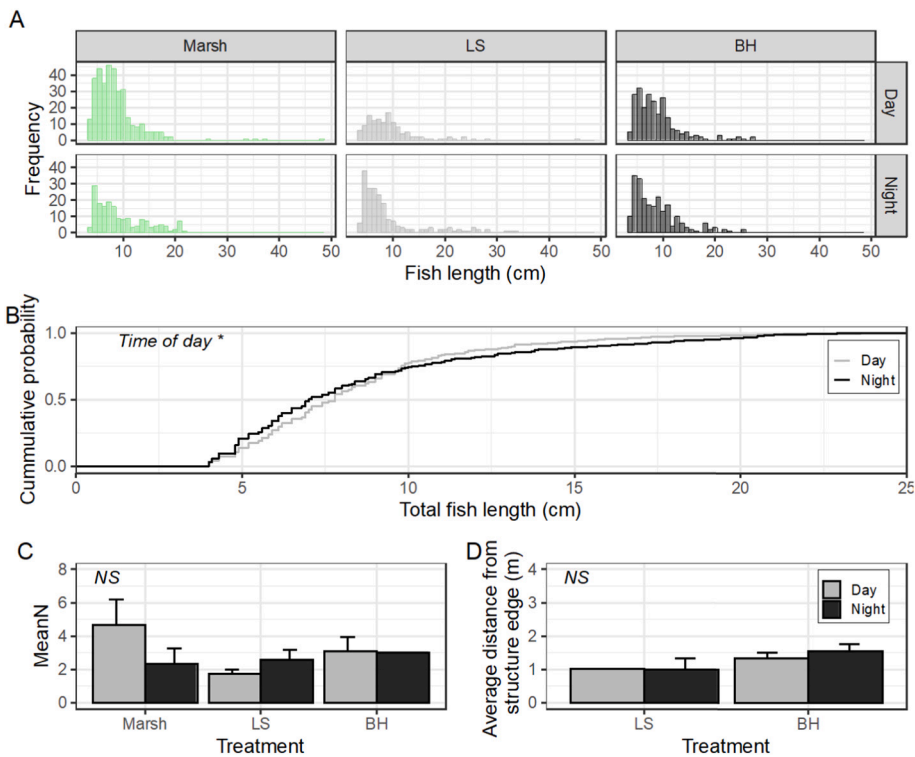


Fig. 7. Metrics from day/night DIDSON fish sampling. (A) Shows the size frequency distribution of all fish across shoreline types and time of day. (B) Shows the cumulative size frequency distribution curves for day versus night; the x-axis has been truncated to highlight the differences between treatments (23 length records are not shown as they exceeded 25 cm). (C) Shows the average number of fish detections (meanN) by shoreline type and time of day. (D) Shows the average distance between fish and the structure edge along living shoreline and bulkheads shorelines and by time of day. Bars show mean \pm SE (n = 3 regions). M = natural reference marsh, LS = living shoreline, and BH = bulkhead.

the shallowest, followed by living shorelines, and then bulkheads. While revetments and bulkheads tend to be in deeper water, living shorelines are often only possible in areas that have modest shoreline slopes and shallower water and their structure can lead to further shallowing along the shoreline (Smith et al., 2018). This shallower water may make it more difficult for larger fish, who may prey upon smaller fish, to get

close to the structure, which could be one mechanism contributing to the nursery value of living shorelines.

Our results, in conjunction with previous studies (Balouskus and Targett, 2016; Gittman et al., 2016a), suggest that fish enhancement along living shorelines may be localized or limited to the natural component of the living shoreline (i.e., saltmarsh) rather than the gray

structural component (i.e., breakwater). However, it is likely that the breakwater itself is increasing the refuge of the marsh and therefore its nursery value by: 1) providing a physical barrier that limits predator access to the marsh or marsh edge; or, 2) increasing sedimentation and maintaining a shallow water habitat that is difficult for predatory fish to access (Currin et al., 2008b; Smith et al., 2018). While the term “living shoreline” can refer to a variety of different nature-based infrastructure techniques, spanning the spectrum from highly “green” (e.g., marsh plantings alone) to more “gray” (e.g., marsh plantings in conjunction with an engineered breakwater), our study investigated fish use of a relatively “gray” type of living shoreline (Smith et al., 2020). More highly engineered living shorelines are often necessary in high energy areas of increased wave action or boat traffic, where marsh plantings alone would not be able to survive (Sutton-Grier et al., 2015). Nevertheless, the trade-off associated with incorporating gray infrastructure into a living shoreline design should be carefully considered and minimized where applicable because the natural habitat components of the living shoreline likely confer the greatest ecological benefit. Natural shorelines have repeatedly been shown to promote fish community stability adjacent to the shoreline and on a cumulative landscape scale (Bilkovic and Roggero, 2008; Scyphers et al., 2015; Kornis et al., 2018); thus, from an ecological perspective, maintaining landscapes that are as natural as possible is likely to be the best option moving forward.

In our temporally limited day/night DIDSON comparison, across all shoreline types, we did not detect any difference in fish abundance during daytime versus nighttime sampling. This result differs from our hypothesis of increased nighttime abundance which was based on previous research showing multifold enhancement of fish catches in nighttime net or trap-based samples (Rountree and Able, 1993; Beauchamp et al., 1994; Guest et al., 2003), including a study conducted in the same area as ours also comparing fish use of natural and bulkhead shorelines (Young, 2017). Young (2017) used gill nets and fyke nets to sample fish use of natural and bulkhead shorelines in NC and recorded nearly twice the abundance of fish during nighttime versus daytime sampling with both gear types. Young (2017) attributed the higher catches of fish at night to either behavioral differences (in foraging, predator avoidance, or reproduction) or to visual gear avoidance during the day. As compared to net, trap, or snorkel/diver surveys, DIDSON sampling efficiency is not as likely to be biased by light availability (as diver surveys might be), nor presumably by fish avoidance behavior which is stronger during the day than at night (Rakowitz et al., 2012). Moreover, in order for the DIDSON to detect a fish, the fish merely needs to enter the area that is being surveyed; in contrast, traditional fish sampling gear must also catch the fish in order for it to be detected. Thus, it is possible that a lack of gear avoidance in our study is responsible for the higher number of fish detections during the day; however, our short sampling window (five minutes) is not directly comparable to netting studies that have soak times of several hours and our limited temporal replication (i.e., one sampling event) do not enable us to make any strong conclusions from these data. Additional studies that use DIDSON in conjunction with traditional fish sampling methods (sensu Rakowitz et al., 2012) may be able to disentangle the advantages and disadvantages of traditional versus novel fish sampling techniques across different light gradients.

DIDSON technology was only introduced to the commercial market in 2002 (Belcher et al., 2002) and it has not been used extensively in shallow-water habitats. DIDSON has the potential to overcome some of the weaknesses associated with traditional gears, namely that it can sample equally well across different light and turbidity regimes and it has been able to detect fish in complex habitats that were otherwise missed by traditional video and diver surveys (Frias-Torres and Luo, 2009; Martignac et al., 2015). Thus, we see a huge potential for using DIDSON to investigate applied and basic ecological questions about the interaction between habitat use and light gradient (sensu Becker et al., 2013). Nevertheless, we did encounter some difficulties while using the DIDSON to pursue research questions in our study system. First,

DIDSONs have more often been used to study the behavior and movement of large fish (Boswell et al., 2008; Burwen et al., 2010; Kang, 2011; Hightower et al., 2013). In contrast, the majority of the fish at our sites were small (< 10 cm), and we are potentially underestimating the small/juvenile fish community in our study because we set a detection threshold of 4 cm. Second, detecting and identifying fish in DIDSON imagery often relies on movement of fish and contrast with background structure and will miss fish that are hiding in the interstices of the structure (Frias-Torres and Luo, 2009). As such, total fish abundances at marshes and living shorelines in our study are likely underestimated because fish are likely to be using the marsh platform and hiding among rocks in the breakwater, particularly around high tide when we conducted DIDSON sampling. In contrast, along bulkhead shorelines we were imaging the entire available habitat because there was nowhere for the fish to hide. Finally, studies with a DIDSON or other imaging sonars that predominantly use abundance metrics may miss changes in overall community composition, which is difficult to determine with the DIDSON as fish species identification is not possible unless the species is morphologically distinct (Martignac et al., 2015). Despite some limitations, imaging sonars, like the DIDSON, can be a powerful tool for investigating fish use and behavior in shallow turbid estuarine environments, and future software advances that optimize the automatic processing of videos may be able to lower processing time and resolve some of the difficulties we experienced (Petreman et al., 2014). Ultimately, using multiple fish sampling techniques in tandem may be a good approach going forward as different methods tend to provide different information about the fish community.

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 A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2021.106232>.

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