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.

Keywords: Sonar; DIDSON; nature-based infrastructure; living shoreline; bulkhead; saltmarsh

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 & MacArthur 1961; 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 & Stein 1982; Heck & Crowder 1991; Eklöv P. & Diehl S. 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 (USACE 2016). Shoreline hardening often results in

69 the replacement of a complex shallow-water habitat (e.g., saltmarsh, mangrove, rocky intertidal)
70 with a more homogenous structure (e.g., smooth vertical seawall) (Bulleri & Chapman 2010).
71 This reduction in shoreline complexity has been associated with decreased biodiversity (Bilkovic
72 & Roggero 2008; Gittman et al. 2016b; Kornis et al. 2018) and altered community dynamics
73 such as species interactions and prey selection (Jackson et al. 2008; Munsch et al. 2017).
74 In response to widespread shoreline hardening, there has been a growing desire to
75 incorporate habitat restoration into shoreline protection schemes to enhance social and ecological
76 resilience and to maintain critical ecosystem services (Dafforn et al. 2015a; Sutton-Grier et al.
77 2015). The result has been the promotion of natural or nature-based infrastructure that includes
78 the conservation or restoration of natural ecosystems with or without added structural
79 components (Dafforn et al. 2015b; Smith et al. 2020). A common nature-based infrastructure
80 design used in the United States includes an offshore breakwater or restored oyster reef (made
81 from granite rocks, marl, or bagged/loose oyster shell) in combination with existing or planted
82 marsh grasses landward of the breakwater (hereon referred to as a living shoreline; USACE
83 2016b). Living shorelines can maintain the coastal ecosystem services provided by saltmarshes
84 and oyster reefs, while also providing increased protection from erosion due to wave action,
85 storm events, and boat wakes (Manis et al. 2015; Smith et al. 2018; Chowdhury et al. 2019).
86 Furthermore, living shorelines preserve or enhance natural habitat heterogeneity via the intertidal
87 breakwater that replaces soft bottom where structure was previously limited, and increasing the
88 heterogeneity of marine infrastructure has been shown to enhance biodiversity (Strain et al.
89 2018). However, unvegetated soft bottom is an important habitat in and of itself, and the merits
90 of replacing soft-bottom with an artificial breakwater or restored oyster reef is a topic of debate
91 (Bilkovic & Mitchell 2013). Nevertheless, the combination of different structural habitat

92 elements within a living shoreline may expand the functional role that living shorelines can play
93 in the coastal environment (Erdle et al. 2006).
94 In contrast to the widely reported detrimental effects of hardened shorelines, recent
95 studies have shown that fish abundances are maintained and in some cases even enhanced along
96 living shorelines as compared to natural shorelines (Currin et al. 2008a; Scyphers et al. 2011;
97 Balouskus & Targett 2016; Gittman et al. 2016a). This may be a function of the increased
98 structural complexity associated with the breakwater (Jennings et al. 1999) that acts to attract or
99 produce fish by providing increased access to refuge, prey, or substrate. Despite these
100 preliminary findings, fish use of the oyster reef and breakwater structures have rarely been
101 sampled and little is known about the mechanism(s) driving the higher observed abundances.
102 Estuarine fish living in complex intertidal habitats are notoriously hard to sample (Rozas
103 & Minello 1997), particularly when comparing across habitats of different complexities or across
104 different light regimes. In the last two decades, use of underwater video for fish sampling has
105 become more prevalent thanks to improved technology, better access to such technology, and
106 potential advantages over traditional methods (e.g., nets, seines, trawls, diver surveys, etc.),
107 specifically that videos are non-extractive, non-invasive, and easy to replicate (Mallet & Pelletier
108 2014). However, one notable limitation of traditional video footage (e.g., GoPROs) is that
109 turbidity in shallow subtidal estuarine habitats is typically high, which inhibits the detection of
110 fish under certain conditions. Few techniques exist which can be used to sample the fish
111 community equally regardless of structure, light limitations, or turbidity.
112 In this study, we used traditional fish sampling gear (i.e., fyke nets and minnow traps) in
113 addition to a Dual-frequency Identification Sonar (DIDSON; Sound Metrics Corporation,
114 Bellevue, WA) to determine whether shoreline type in a shallow suburban estuary has an effect

115 on fish abundance and other community metrics. DIDSONs are portable "acoustic cameras" that
116 can collect video quality images in shallow water settings (Becker et al. 2011; Martignac et al.
117 2015), but they use sound instead of light to image, and thus are not limited by light availability
118 or turbidity. Based on previous research, we hypothesized in this study that: i) fish abundance,
119 biomass, and species richness would be highest at living shoreline sites and lowest at bulkheads
120 (Scyphers et al. 2011; Gittman et al. 2016a); and, ii) the abundance of fish across all shorelines
121 would be higher at night than during the day (Rountree & Able 1993; Beauchamp et al. 1994;
122 Guest et al. 2003; Erika Young 2017). Furthermore, we were interested in using the DIDSON to
123 investigate some of the potential mechanisms underlying the fish enhancement that has been
124 observed in other living shoreline studies. Past studies have speculated that higher fish
125 abundances at living shoreline and natural shoreline sites could be a function of the increase in
126 structural complexity or multiple habitat components (Erdle et al. 2006) providing greater spatial
127 refuge or superior access to food via the colonization of the sill with epibionts and epifauna
128 (Gittman et al. 2016a). Thus, we also hypothesized that: iii) structural affinity (i.e., association
129 between fish and the structure, using distance as a proxy) would be strongest along shorelines
130 that were more complex (i.e., living shorelines) and weakest along shorelines that were more
131 homogenous (i.e., bulkheads); and, iv) structural affinity would be stronger during daylight hours
132 when prey are more vulnerable to visual detection by predators.
133
134 **2. Methods.**
135 *2.1 Site descriptions*
136 To investigate fish use of natural and modified estuarine shorelines, we conducted two
137 independent studies in the summers of 2016 and 2017 in eastern North Carolina. The first study

138 (hereafter referred to as fyke net sampling) used fyke nets to measure fish use of the marsh
139 platform at natural reference marsh sites (Figure 1A) and paired living shorelines (Figure 1B).
140 The sites were grouped in four geographic regions, each with one living shoreline and one
141 reference marsh: Hatteras (35°13'18.8"N 75°41'35.9"W), Bogue Banks (BB; 34°42'12.4"N
142 76°48'21.0"W), Jones Island (JI; 34°41'52.1"N 77°06'26.7"W), and Morris Landing (ML;
143 34°28'11.4"N 77°30'28.3"W) (Figure 2). All living shoreline sites were composed of an offshore
144 sill (i.e., breakwater) made from either granite rocks or bagged oyster shell and planted with
145 *Spartina alterniflora* marsh grass landward of the sill (Table 1). The sill at JI was largely buried
146 under new sediment, but the oysters that had recruited to the sill were still apparent along the
147 shoreline. All reference marshes were dominated by *S. alterniflora* and located within 500 m of
148 the living shoreline sites (Table 1). Fyke nets were set to sample the marsh platform (i.e., the
149 area landward of the sill) and were placed at dropdowns or gaps in the sill (Figure 3).
150 The second study (hereafter referred to as DIDSON sampling) was conducted in the
151 summer of 2017 at nine sites in Carteret County, NC and included sampling with the DIDSON
152 and minnow traps. Sites were geographically grouped within the following three regions: Duke
153 University Marine Lab (Duke; 34°43'07.8"N 76°40'23.2"W); Pine Knoll Shores (PKS;
154 34°42'12.4"N 76°48'21.0"W); and the Pine Knoll Shores Aquarium (AQ; 34°42'04.2"N
155 76°49'54.6"W)(Figure 2). Each region contained one natural marsh, one living shoreline, and one
156 bulkhead (Figure 1). The living shoreline sampled in PKS was the same as the living shoreline
157 sampled in BB in the Fyke Net Study, but all other sites were unique. All living shorelines had a
158 granite breakwater and were planted with *S. alterniflora.* Construction dates for bulkheads are
159 unknown, but all are composed of vinyl sheet pile (Table 1). The corrugation interval on the PKS
160 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 (Figure 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 1m x 1m x 5m central mesh bag (3 mm mesh), with wings (1m x 5m) 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 hour 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

184 temporal replicate and thus these data should be interpreted as preliminary. We used the high-
185 frequency (1.8 Hz) mode on the DIDSON, which is best for collecting high-resolution imagery at
186 short distances (< 12 m). Furthermore, we used a specialized 8-degree concentrator lens (Ocean
187 Marine Industries) to reduce refraction from the water surface and optimize the view field in
188 shallow water. The DIDSON was mounted on an aluminum frame and deployed 5 m from the
189 edge of each shoreline facing towards the shoreline (Figure 3; see Supplementary Figure 1 for an
190 example of DIDSON imagery). We used the real-time viewing in DIDSON software to confirm
191 the correct distance and orientation. The DIDSON sampling required a water depth of
192 approximately 0.5 m, so we limited our sampling window to the two hours around high tide. For
193 each sampling event, we sampled for a total of 10 minutes, including a 5-minute acclimation
194 period after the DIDSON was placed (which is considered an appropriate amount of time for fish
195 to return after a disturbance; Graham 1992), followed by 5 minutes of footage that were used for
196 analysis (with an approximate frame rate of eight frames per second). For the day/night
197 sampling, each site was sampled during the day and at night within the same 24-hour period.
198 Identification of fish species in our study system using DIDSON alone is difficult or
199 impossible unless the species of interest is morphologically distinct. To address this, we also set
200 replicate unbaited minnow traps (n = 5) along the outside edge of each shoreline. Minnow trap
201 sampling was conducted within 24 hours of daytime DIDSON sampling (but not simultaneously,
202 so as not to interfere with the viewing window) during four of the sampling dates at each site.
203 Minnow traps were primarily indexing the small fish species, as the largest fish we caught in our
204 traps was 8.5 cm, therefore minnow trap catches are likely not representative of the full fish
205 community observed with the DIDSON. Traps were set two hours before high tide and pulled
206 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 hour 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-minute 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-minute 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 Figure 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.

252 DIDSON data were analyzed separately as daytime fish counts (aggregate of all daytime
253 videos) and day/night fish counts (only the nighttime videos and daytime videos that were taken
254 within 24 hours of the nighttime videos). To calculate fish structural affinity, we used distance
255 between the fish and the structure edge as a proxy. This comparison was only conducted at
256 bulkhead and living shoreline sites because the edge of natural marsh shorelines was not easily
257 defined. Distance was calculated by measuring the distance between the DIDSON transducer and
258 the structure edge and then subtracting the distance between each fish and the transducer (note
259 that it was possible to have negative distance numbers if the fish were observed past the edge of
260 the structure).
261
262 *2.5 Statistical analysis*
263 To analyze the fyke net data, we first used Generalized Linear Mixed Effects Models
264 (GLMMs; Bolker et al. 2009) to model fish abundance and fish species richness. For each model,
265 treatment (categorical with two levels: marsh and living shoreline) and region (categorical with
266 four levels: Hatteras, BB, JI, ML) were included as fixed effects, and a grouping factor that
267 controlled for repeated measurements over time at the same sites was included as a random
268 effect (i.e., Site ID; 8 levels). The models were fit using the 'glmmTMB' package (Brooks et al.
269 2017). We compared model fit using AIC among Poisson, Generalized Poisson, and negative
270 binomial distributions to find the best fit for the data. Once we selected the final distribution, we
271 used Likelihood Ratio Tests (LRTs) to assess the associations between the response variables
272 and predictor variables (treatment and region) for each model. To model fish biomass, which was
273 a continuous response rather than discrete as above, we used Linear Mixed Effects Models
274 (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; $\chi^2 = 10.58$, $p = 0.001$) and significantly different among regions ($\chi^2 = 8.02$, $p = 0.046$)(Figure 4A). Fish biomass was not significantly different between treatments (LMM; $F = 5.63$, $p = 0.10$) or

321 regions (LMM; F = 2.18, p = 0.27)(Figure 4B). Species richness was significantly higher at
322 living shoreline sites versus reference marsh sites (GLMM; $\chi^2 = 10.58$, p = 0.001) and also
323 significantly different among regions ($\chi^2 = 8.02$, p = 0.046)(Figure 4C; Supplementary Tables 1
324 & 2; Supplementary Figure 3).
325
326 *3.2 Minnow trap sampling*
327 For the minnow trap sampling, across all sampling dates and sites we caught five species
328 of fish along natural shorelines (Mummichog [*Fundulus heteroclitus*], naked goby [*Gobiosoma*
329 *bosc*], pinfish, oyster toadfish [*Opsanus tau*], and pigfish [*Orthopristis chrysoptera*]), three
330 species along living shorelines (mummichog, pinfish, and pigfish), and only two species of fish
331 along bulkhead shorelines (pinfish and pigfish; Table 3). More individuals were caught along
332 natural shorelines as compared to living shorelines and bulkhead shorelines, but these differences
333 were not statistically significant by treatment (GLMM; $\chi^2 = 5.50$, p = 0.06) or region ($\chi^2 = 2.50$, p
334 = 0.29)(Figure 5A). Total fish biomass was not significantly different by treatment (LMM; F =
335 0.39, p = 0.70) or region (F = 0.35, p = 0.72)(Figure 5B). There were no differences in fish
336 species richness among shoreline types (GLMM; $\chi^2 = 1.5$, p = 0.47) or regions ($\chi^2 = 0.25$, p =
337 0.89)(Figure 5C; Supplementary Tables 1 & 2; Supplementary Figure 4).
338
339 *3.3 DIDSON daytime sampling*
340 Across all daytime videos and sampling dates we recorded 1,590 fish in front of bulkhead
341 shorelines, 1,531 fish in front of marsh shorelines, and 1,125 fish in front of living shorelines.
342 The vast majority of fish detected with the DIDSON were small (< 20 cm); only 39 fish were
343 longer than 20 cm and the longest individual was 71 cm (Figure 6A). The cumulative length

distribution of all fish pooled along bulkhead shorelines was significantly different than along living shorelines ($p < 0.001$) and natural marsh shorelines ($p < 0.001$). Length distributions were not statistically different between natural marsh and living shorelines ($p = 0.22$)(Figure 6B). Fish counts were not statistically different among treatments ($F = 1.08$, $p = 0.42$), but there was a marginally significant difference among regions ($F = 6.67$, $p = 0.05$)(Figure 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 ($F = 3.44$, $p = 0.23$)(Figure 6D; Supplementary Table 2; Supplementary Figure 5).

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 (Figure 7A). The cumulative length distribution of all fish pooled was significantly different between day and night samples ($p = 0.02$) with a higher probability of detecting small fish at night (Figure 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 ($F_{2,12} = 2.06$, $p = 0.17$)(Figure 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 ($F_{1,8} = 0.38$, $p = 0.56$)(Figure 7D; Supplementary Table 3).

4. Discussion

366 Our surveys of the marsh platform behind the sill at living shoreline sites showed higher
367 fish abundances and higher fish species richness than natural reference marshes, supporting our
368 main hypothesis. However, our surveys of the shallow subtidal area seaward of marsh, living
369 shoreline, and bulkhead sites did not show any significant differences among shoreline types,
370 though the minnow trap and DIDSON surveys had more limited temporal replication than the
371 fyke net sampling. Our results, in conjunction with similar studies, suggest that the nursery
372 enhancement observed at living shoreline sites may be restricted to the marsh platform behind
373 the living shoreline breakwater rather than the structural component of the breakwater itself.
374 Previous sampling of the fish community at living shoreline sites versus natural reference
375 marshes has typically been designed to sample either: 1) the unvegetated area seaward of the
376 shoreline (Balouskus & Targett 2016); or, 2) use of the marsh platform or area behind the living
377 shoreline breakwater (Currin et al. 2008a; Scyphers et al. 2011). In one study that sampled both
378 the unvegetated area landward of the shoreline and use of the marsh platform, the findings
379 differed between the two sampling designs (Gittman et al. 2016a). In that study, sampling of the
380 marsh platform with fyke nets revealed significantly higher fish abundances and fish diversity
381 along living shorelines than natural shorelines. Similarly, our fyke net catches from the marsh
382 platform behind living shorelines showed higher fish catches and species richness, which
383 provides further support for the hypothesis that installing a living shoreline can enhance the
384 nursery value of eroding marsh shorelines. In contrast, when Gittman et al. (2016) used seine
385 nets to sample the unvegetated area seaward of the shoreline at the same sites as above, they
386 found no significant differences in the fish community among shoreline types. It is worth noting
387 here that catch is a reflection of both abundance and catchability, and it is possible that higher

388 catches are due to the selectivity of different gear types or the catchability of fish in different
389 environments, rather than a true reflection of their abundance (Bacheler & Shertzer 2020).
390 Contrary to the fyke net data, our minnow trap sampling at living shoreline, bulkhead,
391 and natural marsh sites did not find any significant differences in fish catches or biomass. It is
392 notable that Gittman et al. (2016a) also used minnow traps to sample marsh, living shoreline, and
393 bulkhead sites in NC and caught significantly more fish at living shoreline sites than bulkhead
394 sites. We attribute this inconsistency between our studies to the fact that: 1) Gittman et al.
395 (2016a) used ten minnow traps per site (versus our five) and thus had more statistical power for
396 detecting differences; and, 2) minnow traps in that study were set behind the sill, rather than in
397 front of the sill as in our study. Minnow traps behind the breakwater are presumably sampling
398 both fish use of the breakwater itself and fish use of the refuge and marsh behind the breakwater,
399 whereas our minnow traps on the outside of the breakwater were testing fish use of the structural
400 component of the breakwater alone. In contrast, Balouskus and Targett (2016) used minnow
401 traps to sample the seaward edge of marshes, living shorelines, and revetments, and similar to
402 our results they did not find enhanced fish abundances or species richness in front of living
403 shorelines. Exclusively sampling along the outside of the breakwater may produce results that
404 are comparable to sampling along a revetment (i.e., a sloping rock shoreline where there is no
405 marsh behind the structure), and while revetments are often ecologically preferable to bulkheads
406 they still typically host fewer organisms than natural shorelines (Erdle et al. 2006; Seitz et al.
407 2006; Bilkovic & Roggero 2008).
408 Similar to the results from the minnow trap sampling, DIDSON sampling did not show
409 any significant differences in fish abundance by shoreline type; however, there were statistical
410 differences in the size frequency distribution of fish between bulkheads and the other two

411 shoreline types. The cumulative length distribution of fish at living shorelines and natural
412 shorelines were more similar than along bulkhead shorelines, where fish tended to be slightly
413 larger; this, in addition to our fyke net sampling, offers further support that living shorelines are
414 providing more suitable habitat for small fish. Kornis et al. (2018) found similar results when
415 sampling the shallow subtidal area seaward of natural, bulkhead, and revetment shorelines in the
416 Chesapeake Bay. The authors found that fish tended to be larger along bulkhead and revetment
417 shorelines than along natural shorelines. The fact that living shorelines and marshes had similar
418 size frequency distributions in our study may be a reflection of water depth. Our natural marsh
419 sites were the shallowest, followed by living shorelines, and then bulkheads. While revetments
420 and bulkheads tend to be in deeper water, living shorelines are often only possible in areas that
421 have modest shoreline slopes and shallower water and their structure can lead to further
422 shallowing along the shoreline (Smith et al. 2018). This shallower water may make it more
423 difficult for larger fish, who may prey upon smaller fish, to get close to the structure, which
424 could be one mechanism contributing to the nursery value of living shorelines.
425 Our results, in conjunction with previous studies (Balouskus & Targett 2016; Gittman et
426 al. 2016a), suggest that fish enhancement along living shorelines may be localized or limited to
427 the natural component of the living shoreline (i.e., saltmarsh) rather than the gray structural
428 component (i.e., breakwater). However, it is likely that the breakwater itself is increasing the
429 refuge of the marsh and therefore its nursery value by: 1) providing a physical barrier that limits
430 predator access to the marsh or marsh edge; or, 2) increasing sedimentation and maintaining a
431 shallow water habitat that is difficult for predatory fish to access (Currin et al. 2008b; Smith et
432 al. 2018). While the term "living shoreline" can refer to a variety of different nature-based
433 infrastructure techniques, spanning the spectrum from highly "green" (e.g., marsh plantings

434 alone) to more “gray” (e.g., marsh plantings in conjunction with an engineered breakwater), our
435 study investigated fish use of a relatively “gray” type of living shoreline (Smith et al. 2020).
436 More highly engineered living shorelines are often necessary in high energy areas of increased
437 wave action or boat traffic, where marsh plantings alone would not be able to survive (Sutton-
438 Grier et al. 2015). Nevertheless, the trade-off associated with incorporating gray infrastructure
439 into a living shoreline design should be carefully considered and minimized where applicable
440 because the natural habitat components of the living shoreline likely confer the greatest
441 ecological benefit. Natural shorelines have repeatedly been shown to promote fish community
442 stability adjacent to the shoreline and on a cumulative landscape scale (Bilkovic & Roggero
443 2008; Scyphers et al. 2015; Kornis et al. 2017); thus, from an ecological perspective, maintaining
444 landscapes that are as natural as possible is likely to be the best option moving forward.
445 In our temporally limited day/night DIDSON comparison, across all shoreline types, we
446 did not detect any difference in fish abundance during daytime versus nighttime sampling. This
447 result differs from our hypothesis of increased nighttime abundance which was based on
448 previous research showing multifold enhancement of fish catches in nighttime net or trap-based
449 samples (Rountree & Able 1993; Beauchamp et al. 1994; Guest et al. 2003), including a study
450 conducted in the same area as ours also comparing fish use of natural and bulkhead shorelines
451 (Young 2017). Young (2017) used gill nets and fyke nets to sample fish use of natural and
452 bulkhead shorelines in NC and recorded nearly twice the abundance of fish during nighttime
453 versus daytime sampling with both gear types. Young (2017) attributed the higher catches of fish
454 at night to either behavioral differences (in foraging, predator avoidance, or reproduction) or to
455 visual gear avoidance during the day. As compared to net, trap, or snorkel/diver surveys,
456 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 & 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

480 in our study because we set a detection threshold of 4 cm. Second, detecting and identifying fish
481 in DIDSON imagery often relies on movement of fish and contrast with background structure
482 and will miss fish that are hiding in the interstices of the structure (Frias-Torres & Luo 2009). As
483 such, total fish abundances at marshes and living shorelines in our study are likely
484 underestimated because fish are likely to be using the marsh platform and hiding among rocks in
485 the breakwater, particularly around high tide when we conducted DIDSON sampling. In contrast,
486 along bulkhead shorelines we were imaging the entire available habitat because there was
487 nowhere for the fish to hide. Finally, studies with a DIDSON or other imaging sonars that
488 predominantly use abundance metrics may miss changes in overall community composition,
489 which is difficult to determine with the DIDSON as fish species identification is not possible
490 unless the species is morphologically distinct (Martignac et al. 2015). Despite some limitations,
491 imaging sonars, like the DIDSON, can be a powerful tool for investigating fish use and behavior
492 in shallow turbid estuarine environments, and future software advances that optimize the
493 automatic processing of videos may be able to lower processing time and resolve some of the
494 difficulties we experienced (Petreman et al. 2014). Ultimately, using multiple fish sampling
495 techniques in tandem may be a good approach going forward as different methods tend to
496 provide different information about the fish community.
497
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510

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680

Table 1. Description of study sites. Mean depths show mean ± 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 ± 5 (4)	23 ± 3 (4)
Hatteras	LS	Granite	2011	< 0.5 m	41 ± 4 (4)	34 ± 3 (4)
BB	Marsh			0.5 – 1 m	81 ± 6 (4)	16 ± 1 (4)
BB	LS	Granite	2012	0.5 – 1 m	61 ± 8 (4)	8 ± 3 (4)
JI	Marsh			0.5 – 1 m	86 ± 5 (4)	46 ± 3 (4)
JI	LS	Bagged oyster shell	2010	0.5 – 1 m	81 ± 6 (4)	44 ± 5 (4)
ML	Marsh			> 1 m	58 ± 3 (4)	32 ± 5 (4)
ML	LS	Bagged oyster shell	2011	> 1 m	72 ± 3 (4)	43 ± 6 (4)

DIDSON Study

					Mean depth at structure edge (cm)	Mean depth at DIDSON frame (cm)
Duke	Marsh			0.5 – 1 m	43 ± 2 (2)	62 ± 1 (2)
Duke	LS	Granite	2002	0.5 – 1 m	66 ± 6 (2)	105 ± 4 (2)
Duke	BH	Vinyl	After 2002	0.5 – 1 m	90 ± 11 (2)	105 ± 12 (2)
PKS	Marsh			0.5 – 1 m	39 ± 16 (2)	69 ± 16 (2)
PKS	LS	Granite	2012	0.5 – 1 m	53 ± 13 (2)	64 ± 12 (2)
PKS	BH	Vinyl	Unknown	0.5 – 1 m	61 ± 14 (2)	68 ± 12 (2)
AQ	Marsh			0.5 – 1 m	32 ± 17 (2)	62 ± 15 (2)
AQ	LS	Granite	2002	0.5 – 1 m	51 ± 18 (2)	74 ± 10 (2)
AQ	BH	Vinyl	Unknown	0.5 – 1 m	89 ± 14 (2)	97 ± 16 (2)

685 **Table 2. Fyke net species list.** Catches and biomass are reported as means with SE in

686 parentheses (n = 4 regions).

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

687

688 **Table 3. Minnow Trap species list.** Catches and biomass are reported as means with SE in

689 parentheses (n = 3 regions).

	Living Shoreline		Marsh		Bulkhead	
Species (Common name)	Ind/6h	Biomass (g/6h)	Ind/6h	Biomass (g/6h)	Ind/6h	Biomass (g/6h)
Fish						
Lagodon rhomboides (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)
Fundulus heteroclitus (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)
Orthopristis chrysoptera (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)
Gobiosoma bosc (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)
Opsanus tau (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)

690

691 **Figures**

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

695

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

698

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

703

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

707

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

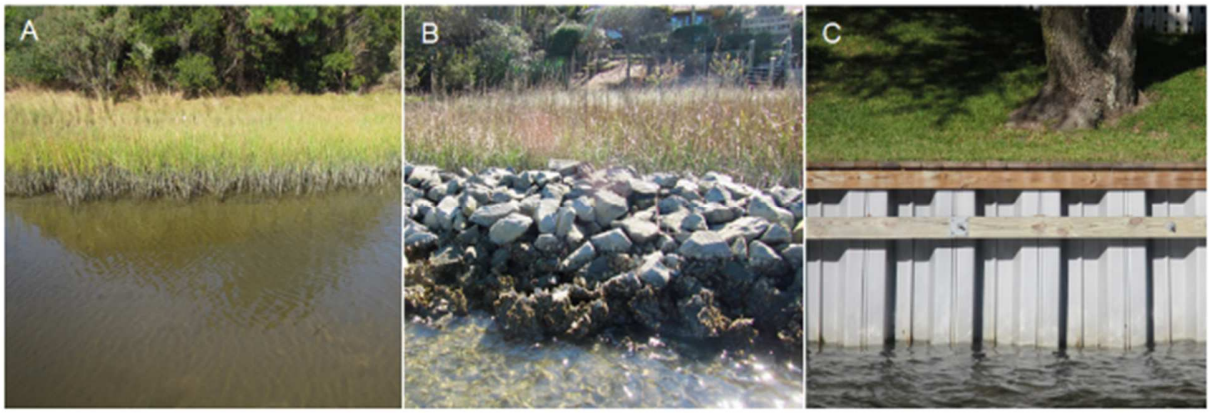
711

712 **Figure 6.** Metrics from daytime DIDSON fish sampling. (A) Shows the size frequency
713 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 ± SE (n=5 sampling dates). M = natural reference marsh, LS = living shoreline, and BH = bulkhead.

Figure 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 verses 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 ± SE (n=3 regions). M = natural reference marsh, LS = living shoreline, and BH = bulkhead.

729 **Figure 1.**



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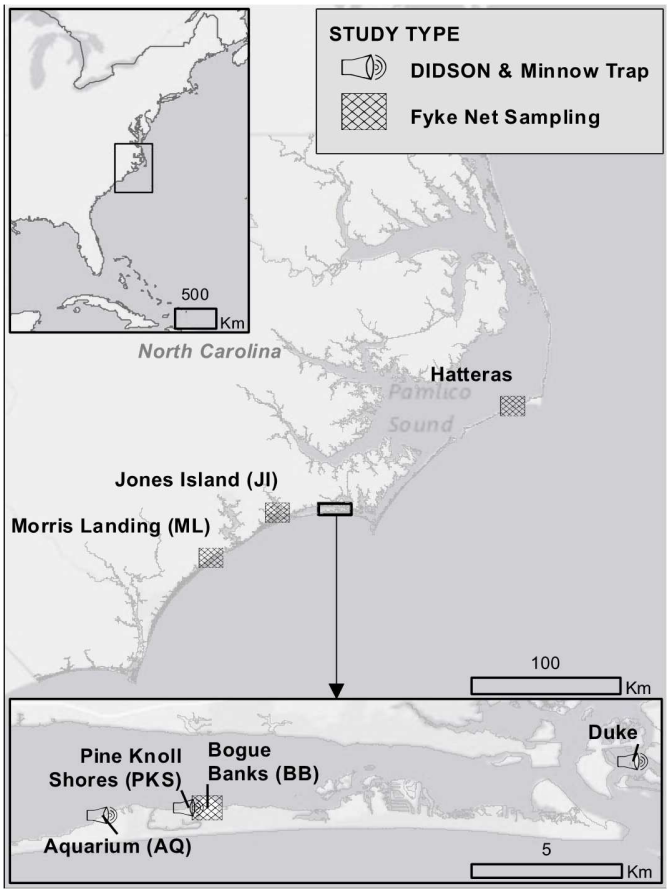

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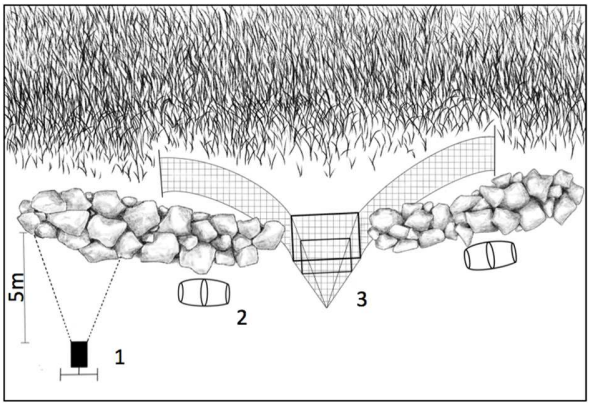

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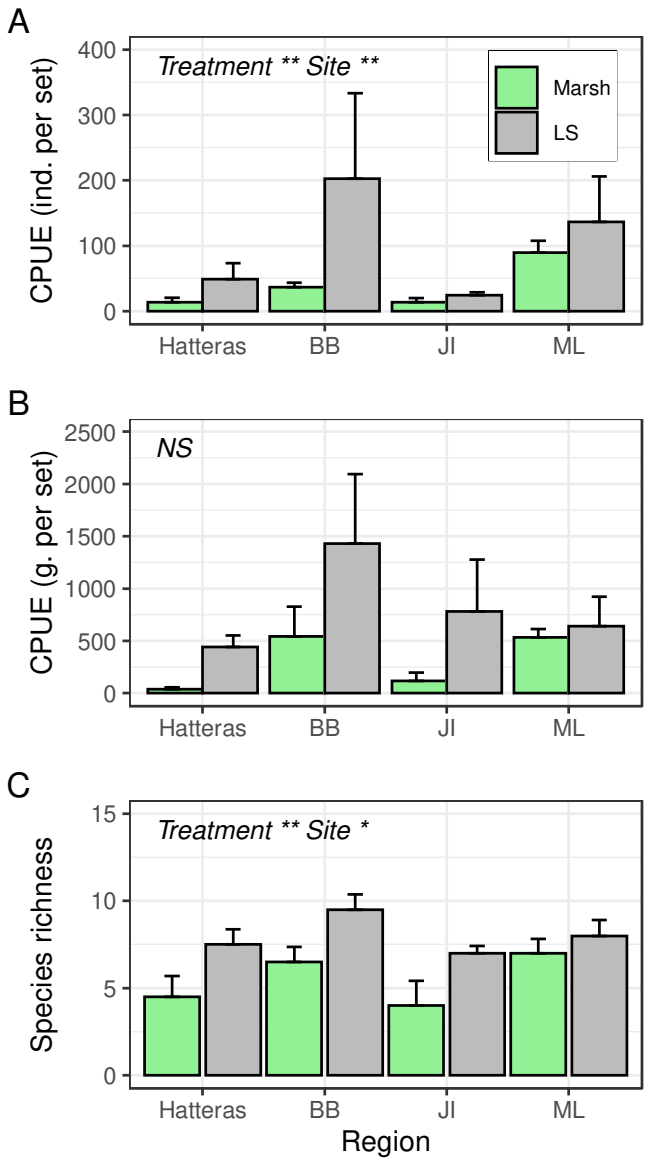
736 **Figure 4.**



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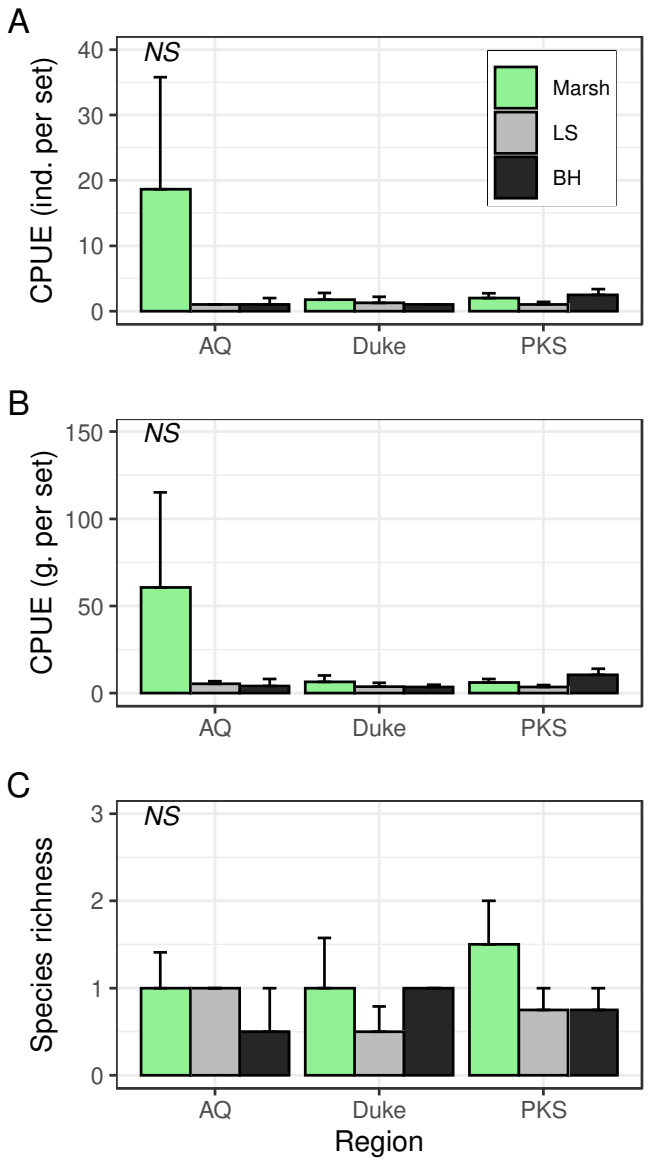

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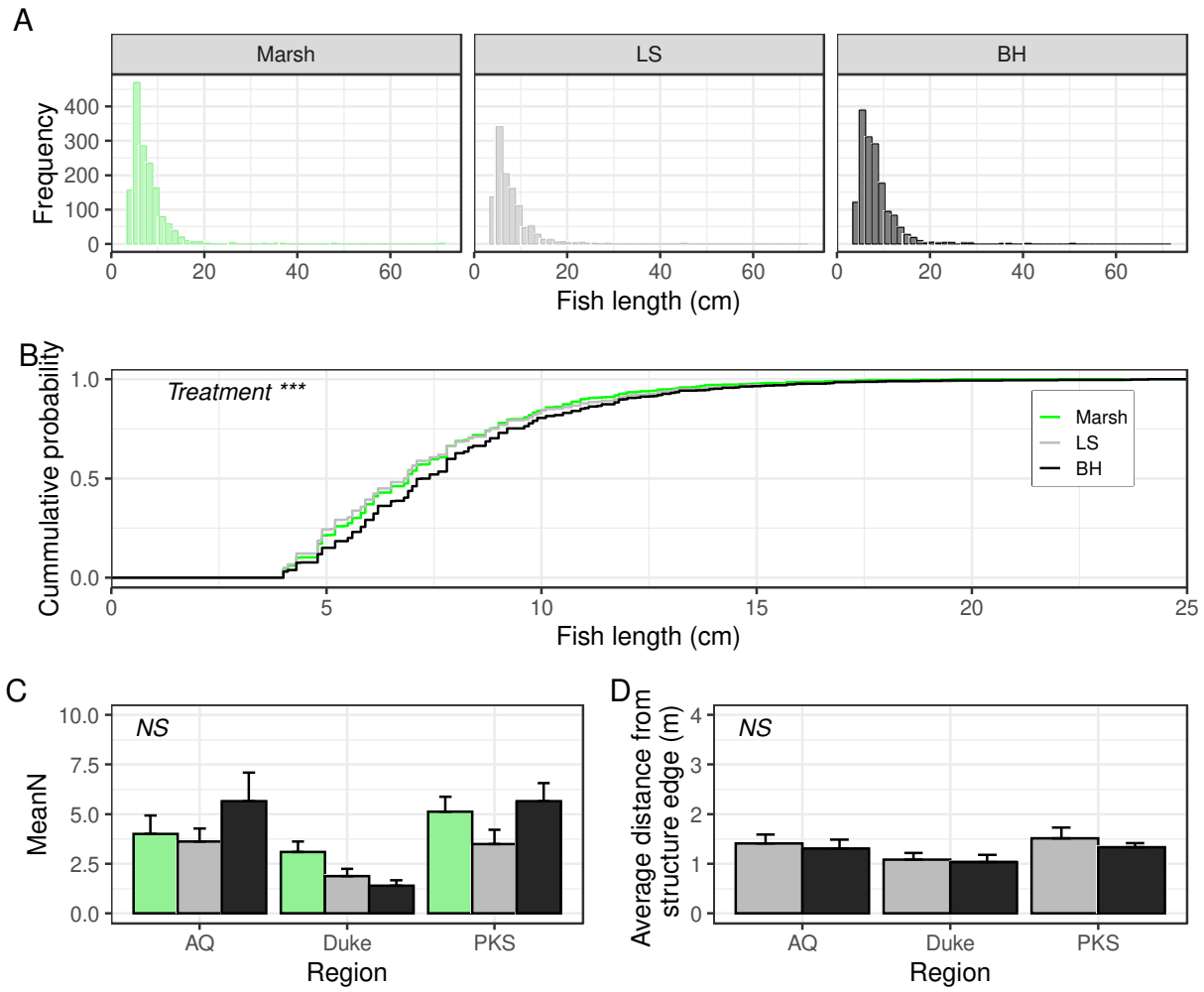

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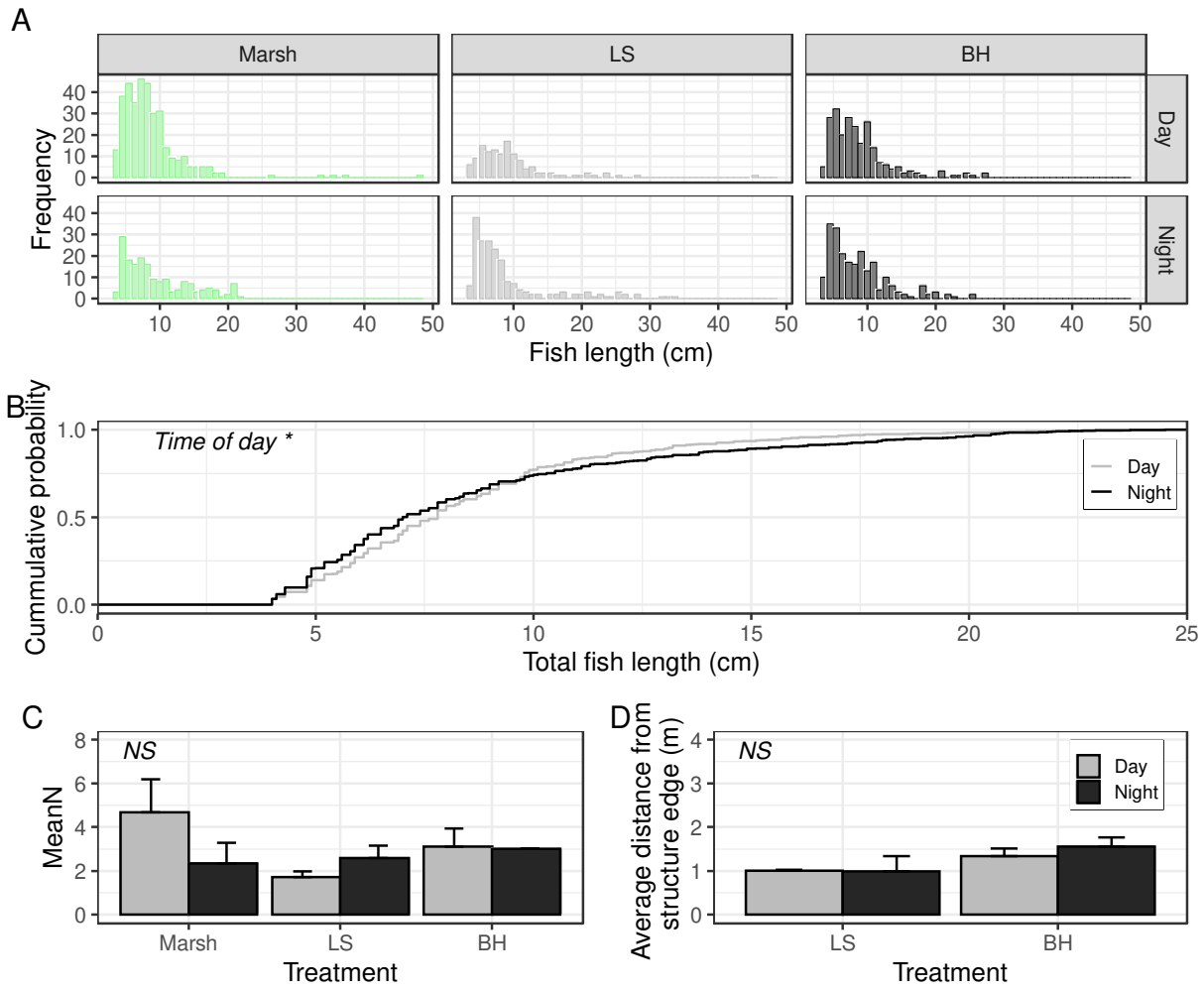
742 **Figure 7.**



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