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NEKTON COMMUNITY RESPONSES TO LIVING SHORELINE RESTORATIONS IN ALABAMA

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INTRODUCTION
Eroding shorelines negatively impact infrastructure, and leads to the loss of critical coastal habitats that provide a variety of ecosystem services (Barbier et al. 2011, Beaumont et al. 2014, Mitsch et al. 2015). With predicted increases in coastal erosion (Mentaschi et al. 2018), nature-friendly coastal restoration techniques such as Living Shorelines (LS) are increasingly replacing traditional shoreline hardening, which causes negative impacts such as decreased habitat quality for nekton (Munsch et al. 2017). Living Shorelines aim to mitigate the impacts of coastal erosion while maintaining ecosystem services of natural shorelines by protecting and encouraging the development of healthy marsh vegetation (Gilby et al. 2021).

Successful LS restoration should ideally transition shorelines from eroding to accreting (Gedan et al. 2011, Polk and Eulie 2018). The increased accessibility of salt marsh vegetation for fish and mobile crustaceans (nekton), availability of structured habitat, and more access to prey resources are among the main features of healthy shorelines, making the enhancement of nekton habitat a co—benefit of LS restoration (Smith et al. 2020). Previous research on nekton community responses to LS restorations has produced varying results. While some studies suggest improved nekton habitat quality (Gittman et al. 2016, Scyphers et al. 2011), others found no difference between restored sites and unrestored controls (Guthrie et al. 2022, de Barros et al. 2023, Legaspi et al. 2023). The variability in results may partly be attributed to the conditions of the control sites in each study, such as whether the control sites were healthy and stable, eroding, or degraded in other ways.

While assessing nekton communities at multiple restored sites in the northern Gulf of Mexico (GOM), de Barros et al. (2023) and Legaspi et al. (2023) suggested that nekton community metrics might be insensitive to subtle effects of restoration on habitat quality, due to the large effort needed to effectively sample these highly variable communities. However, these studies were based on a single season of sampling and may have lacked sufficient replication to detect restoration effects. The present study evaluates patterns in nekton community structure over 2 years among restored, eroding controls, and hardened shorelines in the northcentral GOM. In addition to shoreline status, we also explored a range of environmental variables including dissolved oxygen, temperature, salinity, shoreline type, substrate type, and depth for the purpose of explaining variation in community structure.

MATERIALS AND METHODS
Study sites
We sampled 7 of the largest publicly funded LS restoration projects within Mobile Bay and Mississippi Sound in coastal Alabama during the summers of 2022 and 2023. Each of the 7 LS projects was implemented between 2009 and 2020, with some sites including multiple phases of restoration through time. The projects utilized a variety of breakwater structures and materials, and more detailed site descriptions and a site map are provided in de Barros et al. (2023). de Barros et al. (2023) also sampled the Swift Tract LS on the eastern shore of Mobile Bay, however, due to challenging site conditions, this location was not sampled in 2023, and therefore not included in the present analyses.

As is often the case in shoreline restoration projects, there were no pre—construction nekton monitoring data collected from these sites. We therefore utilized space—for—time substitution by sampling 6 unrestored, eroding control shorelines close to each of the restoration projects. Under this design, restoration that is successful at enhancing degraded habitat should be reflected by enhanced nekton abundance at restored sites (de Barros et al. 2023). One of the control shorelines, Deer River, served as a control for both Saltaire and Helen Wood Park, being the nearest unrestored marsh shoreline with similar exposure to each of these restored sites. We assume the controls represent what restored sites would look like if restoration had not occurred because those sites are undergoing variable rates of erosion and subsidence, often presenting escarped marsh edges (Pickert 1989, Damgaard 2019). We also included 4 rip—rap hardened shorelines to represent the alternative to LS restoration, i.e. traditional shoreline hardening. Therefore, a total of 17 shorelines were sampled for 2 summers. Shorelines were grouped for analyses into single sites when they occurred along immediately adjacent contiguous shorelines (i.e. PaP, CI, ...
AP, LB, SI), and treated as independent sites when they were not, for a total of 13 sites (Figure 1A; as in de Barros et al. 2023). Each seine haul is treated as an independent replicate of nekton communities since they were taken at a considerable distance to each other (≥ 75 m) as in de Barros et al. (2023). Each seine is treated as an independent replicate of nekton communities since they were taken at a considerable distance to each other (≥ 75 m) as in de Barros et al. (2023). 

**Sampling Procedures**

Nekton samples were collected using a 15.2 m center−bag seine with a 6.4−mm stretched mesh and a 1.83 m deep bag. Standardized 100 m² replicates were collected by pulling the seine for 10 m with a headrope ensuring a width of 10 m between seine poles. Seines were pulled parallel to the shoreline with the shoreward end of the net at the marsh edge whenever possible. To ensure that the shoreward end of the net was in water at least 20 cm deep, occasionally the net was hauled up to 20 m from the marsh edge. Between 4 and 12 replicate seine hauls were collected in the summers of 2022 and 2023 from each site based on the length of the LS breakwaters or site extent. Each seine replicate was located at least 75 m apart, usually greater than 100 m, to ensure independence. Sampling was conducted between 7 June and 27 July 2022 (Year 1) and between 23 May and 12 June 2023 (Year 2). All organisms were returned to the laboratory where they were sorted, identified to the lowest practical taxonomic level, and enumerated. All fish sampling followed protocols of the Institutional Animal Care and Use Committee (IACUC) of the University of South Alabama, U.S.A., under protocol #1903663–2.

**Explanatory Variable Assessment**

To further investigate drivers of community variability between our selected sites, we collected the following abiotic variables for each seine haul: dissolved oxygen (mg/ml), temperature (°C), and salinity were taken using a YSI handheld multiparameter instrument; shoreline type (vegetated, escarped, bare, hardened), breakwater type (oyster shell/WADs, rip-rap, Reef Blocks, Reef Balls, Reef Balls/rip-rap, bagged shell, oyster castles/oyster shells), and substrate type (mud/sand, and SAV presence) were noted for each seine haul; and water depth (m) was measured at the start and end of each haul to calculate the average depth of the haul.

To identify environmental variables that may contribute to variation in nekton communities, we obtained wind speed and direction from Alabama’s Real−Time Coastal Observing System (ARCOS), tidal stage from ARCOS or NOAA weather monitoring stations nearest to each sampling site (ARCOS 2011, NOAA 2024), and moon phase from the Farmer’s Almanac (2023).

**Statistical analysis**

To analyze the spatial variation in nekton community composition among LS, control, and hardened sites, we used non−metric Multidimensional Scaling (nMDS) based on Bray−Curtis distance measure with
Nekton Community Responses to Restoration

square-root transformed CPUE data, and Jaccard distance for presence-absence. To test for differences in the nekton community composition between sites and treatments, we conducted a nested factorial PERMANOVA on the Bray–Curtis dissimilarity matrix, after testing for multivariate homogeneity of variances (Anderson 2017). This analysis included an interaction term between the site and treatment factors, with breakwater type and age nested within treatment. Pairwise comparisons were used to detect which pairs of sites and treatments were different from each other using Bonferroni-corrected probability values. The same PERMANOVA was also conducted on finfish-only data due to the high abundances of shrimp possibly driving community patterns even with square-root transformation. We also conducted Similarity Percentage Analyses (SIMPER) to determine which species drive potential variations between treatment types in the nekton community structure (Clarke 1993). Finally, potential effects of environmental variables on community structure were assessed using multiple regressions between environmental variables and nMDS ordination scores. All statistical analyses were conducted with the “vegan” and “pairwiseAdonis” packages (Dixon 2003) in the R environment for statistical computing (R Core Team 2021).

**Results**

We collected 10,579 nekton individuals comprising 71 taxa in a total of 185 replicate seine net hauls. The most abundant taxa throughout the whole dataset were white shrimp *Penaeus setiferus*, brown shrimp *Farfantepenaeus* spp., Atlantic Croaker *Micropogonias undulatus*, Bay Anchovy *Anchoa mitchilli*, Hardhead Catfish *Ariopsis felis*, grass shrimp *Palaemonetes* spp., Silver Perch *Bairdiella chrysoura*, Pinfish *Lagodon rhomboides*, and Spot *Leiostomus xanthurus* (see Table S1 for details on abundance by taxon).

Nekton community composition shows substantial spatial variation among our studied sites, with significant spread in the multivariate space of the nMDS ordinations (Figures 1B, 1C, and S1). Control and LS sites considerably overlap on both presence-absence and abundance-based ordinations, while the hardened sites differed only for the complete dataset (Figures 1B and 1C). Relatively high stress values (> 0.2) suggest that there are considerable distortions in the ordination when representing the community composition (Figure 1B, 1C). The nested PERMANOVA on square-root transformed abundance data confirms the spatial variation in community composition, with significant site (*F*_{12,174} = 5.76, *p* = 0.001) and treatment (*F*_{2,174} = 2.57, *p* = 0.007), but no interaction effects (*F*_{2,174} = 1.004, *p* = 0.43). We also detected no effects of either age (*F*_{1,174} = 0.9, *p* = 0.6) or breakwater type (*F*_{1,174} = 0.96, *p* = 0.48), and the overall model had limited explanatory power (residual *r*² = 0.61). Pairwise comparisons show that the treatment effect is due to hardened shorelines being different from both LS (*F* = 9.67, *p* = 0.003) and controls (*F* = 6.49, *p* = 0.003), while there is no evidence suggesting differences between LS and controls (*F* = 0.014, *p* = 0.072). When crustaceans were excluded from the nested PERMANOVA, nekton communities only varied by site (Figure S1, Table S2). For the complete dataset, the SIMPER analysis showed that the main species driving dissimilarities between hardened vs. control and LS sites are the penaeids *P. setiferus* and *Farfantepenaeus* spp., *M. undulatus*, *A. felis*, *A. mitchilli*, and *L. xanthurus*. Specifically, we found the penaeids *Farfantepenaeus* spp. and *P. setiferus*, as well as anchovies *A. mitchilli* are more abundant at LS and controls than at hardened sites (Table 1). We also found significant effects of salinity, temperature, wind speed, moon phase, SAV presence, and substrate type on nekton abundance and presence across our study sites, but depth did not have a significant effect on eight nekton abundance or presence (Table 2).

**Discussion**

We found no clear differences in the nekton communities between LS and control sites, while the common species in the complete dataset (finfish and shellfish) were all more abundant at LS and control sites than at nearby riprap hardened shorelines. Our research supports previous studies conducted at the same sites, which were based on 1 year of data (de Barros et al. 2023, Legaspi et al. 2023). This study is also consistent with other research that has compared restored and hardened shores (Gittman et al. 2016), and therefore contributes to the growing evidence that habitat quality declines with hardening (Munsch et al. 2017). Since our control sites should resemble the restored sites had they not received restoration, we expected to find higher abundance and diversity at LS restored sites, indicating that restoration was successful at enhancing nekton habitat. However, despite sampling over 2 summers, we did not detect restoration effects, suggesting that the community

<table>
<thead>
<tr>
<th>Species</th>
<th>LS x Hardened</th>
<th>Control x Hardened</th>
<th>CPUE - Control</th>
<th>CPUE - LS</th>
<th>CPUE - Hardened</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Penaeus setiferus</em></td>
<td>12%</td>
<td>12%</td>
<td>33.5</td>
<td>7.5</td>
<td>26.9</td>
</tr>
<tr>
<td><em>Farfantepenaeus</em> spp.</td>
<td>11%</td>
<td>8.5%</td>
<td>14.8</td>
<td>7.1</td>
<td>16.3</td>
</tr>
<tr>
<td><em>Micropogonias undulatus</em></td>
<td>5.4%</td>
<td>5.3%</td>
<td>4.2</td>
<td>5.8</td>
<td>5.2</td>
</tr>
<tr>
<td><em>Ariopsis felis</em></td>
<td>4.7%</td>
<td>4.8%</td>
<td>3.8</td>
<td>4.4</td>
<td>5</td>
</tr>
<tr>
<td><em>Anchoa mitchilli</em></td>
<td>3.7%</td>
<td>4.8%</td>
<td>7.9</td>
<td>3.1</td>
<td>6.4</td>
</tr>
<tr>
<td><em>Leiostomus xanthurus</em></td>
<td>4.1%</td>
<td>3.9%</td>
<td>5.3</td>
<td>5.8</td>
<td>3.7</td>
</tr>
</tbody>
</table>

TABLE 1. Results of the Similarity Percentage (SIMPER) analysis showing the average percent contribution of individual taxa to the dissimilarities between hardened vs. Living Shorelines (LS)/controls and average catch per unit effort (CPUE; individuals/seine haul) in Alabama.
metrics commonly used may not be sensitive to more subtle effects of restoration on highly variable estuarine nekton communities (de Barros et al. 2023). Variation in nekton communities is driven by a wide range of factors at multiple scales, such as recruitment patterns, post—recruitment survival, habitat characteristics and quality (that may be influenced by restoration), and physical environmental conditions (e.g. Davis et al. 2014), meaning it is difficult to detect clear effects of individual restoration projects. Since few projects fund pre—restoration monitoring to establish baseline datasets, we rely on comparison to control sites. Given that each of the sites consists of different environments and restoration projects, it is difficult to design studies to identify effects of restoration that are not confounded with site effects. In our case, a significant amount of variation can be explained by differences among sites. Therefore, interpreting these findings is challenging due to the confounding effects of various site—specific factors.

We found significant effects of various environmental and habitat variables on nekton abundance and composition. Coastal Alabama receives large episodic freshwater discharge events from the Mobile Delta, which creates gradients and dynamic environmental conditions across our study area (Stumpf et al. 1993). However, despite finding significant relationships, the environmental variables generally explain minimal variation in nekton communities, as per the low r² values in Table 2. Even so, it is difficult to interpret these findings since environmental variables were largely confounded with site. Analyzing environmental variables and community assemblages over a larger temporal scale may offer more insights into relevant environmental drivers than sampling in a single season. Additionally, as one of LS main objectives is to buffer wave action at the shoreline, wave energy should also be considered in future studies (e.g. Jordaan 2010).

Since community metrics might be insensitive to detecting the effects of restoration on nekton communities, we reiterate that alternative metrics such as diet, growth, and condition could be incorporated into the toolkit to assess restoration effects (Bilkovic et al. 2016; de Barros et al. 2023). Community metrics are useful for identifying potential indicator species to be explored with alternative metrics (e.g., Legaspi et al. 2023).

While we found that marsh edge nekton communities in restored and control habitats are different from those inhabiting hardened sites, our 2—year dataset could not detect clear differences between restored and unrestored marsh edge habitats. While our study features a comprehensive dataset over multiple sites, the sole use of seine nets limits our ability to fully understand the nekton communities at the studied locations since those are ineffective at sampling marsh—resident species (e.g. Fundulus spp.) More extensive spatial and temporal replication, as well as the use of multiple gears to cover more habitat types, result in detection differences in nekton communities in response to restoration; however, larger—scale nekton sampling is generally beyond the budgets of most restoration monitoring programs (Guthrie et al. 2022). We suggest that alternative metrics should be adopted to determine whether LS are improving habitat quality.

### ACKNOWLEDGMENTS

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