Comparative nekton habitat assessment of eroded-forest, marsh, and beach estuarine shorelines

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ABSTRACT

Dramatic variations in shoreline types create a mosaic of shoreline habitats within estuaries along the U.S. Gulf coast. Previous research has demonstrated shorelines vegetated with marsh plants are associated with higher faunal abundance and diversity relative to non-vegetated habitats. However, an increasingly common, yet understudied, shoreline type is forested, often eroded, shorelines. Within existing habitat mosaics, the structural complexity associated with eroded-forest shorelines could offer unique advantages for supporting specific nekton communities. To assess the comparative shoreline habitat preferences of nekton, three different habitat types (eroded-forest, marsh, beach) were identified in East Bay, Panama City, Florida and nekton communities were assessed with quarterly seine net sampling for one year. Results indicate that community composition and biodiversity patterns were primarily driven by season, with spring exhibiting significantly lower nekton richness and diversity than summer and winter. Shoreline type also influenced community structure with marsh shore-lines consistently supporting higher species richness and diversity than eroded-forests and beaches, though no significant differences in total abundances were detected. These findings support existing literature showing structurally complex habitats such as marshes provide critical resources for estuarine nekton, particularly during summer and winter periods. Results from this study enhanced understanding of the habitat benefits of different shoreline habitat types, offering valuable guidance for restoration efforts and management practices.

1. Introduction

Natural estuarine shorelines are some of the most valuable, yet imperiled ecosystems worldwide (Gittman et al., 2015; Stockdon et al., 2012). The valuable services natural shorelines provide include storm protection (Kemp, 2008; Shaffer et al., 2009), nutrient cycling (Chmura et al., 2003), and habitat for nekton communities (Ross and Lancaster, 2002). Some of the most prominent natural shoreline types found in estuaries along the northern portion of the United States Gulf coast (e.g., Texas to through the panhandle of Florida) are beaches, marshes, and coastal forests, the latter often exhibiting varying degrees of erosion (Geselbracht et al., 2015). Each of these shoreline types are known to provide different ecosystem functions and services, integral to

maintaining ecosystem resilience, particularly providing nekton benefits (Able et al., 2013; Beck et al., 2001).

Beaches provide long stretches of unobstructed habitat functioning as relatively self-contained locations of site fidelity for resident and transient fauna (Hackney et al., 1996). For example, juvenile Florida pompano (*Trachinotus carolinus*) and Gulf kingfish (*Menticirrhus littoralis*) typically exhibit high site fidelity along open ocean beaches, suggesting a self-contained cell where large-scale movements are not justified by predation pressure or limited resources (Ross and Lancaster, 2002). Such habitats provide both refuge and nursery opportunities, making them important for sustaining localized and transient populations. Although research on nekton use of beaches and surf zones is limited (Olds et al., 2018), these habitats are known to support sea

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turtles, crustaceans, and other migratory nekton species, often serving as essential nursery grounds (Able et al., 2013).

Salt marshes provide numerous highly valuable benefits such as carbon sequestration (Chmura et al., 2003), shoreline stabilization (King and Lester, 1995), nutrient filtration (Valiela et al., 2000; Ledford et al., 2021), and habitat creation for important nekton species including a variety of fishes, shrimp, and commercially important crab species (Stamp et al., 2022; Glover et al., 2023). Specifically, these habitats provide the benefit of a secure nursery area with low abundances of large predatory piscivorous fishes (Mathieson et al., 2000; Paterson and Whitfield, 2000). Salt marshes support diverse nekton communities, but nekton are unevenly distributed within these habitats, with edges harboring higher densities than interior areas (Peterson and Turner, 1994; zu Ermgassen et al., 2021). Salt marsh interiors are primarily used by resident species, whereas salt marsh edges may support both resident and transient nekton (Peterson and Turner, 1994). These differences indicate that nekton community composition responded to variation in habitat type and physical structure within estuaries, motivating broader comparisons among distinct shoreline types that differ in vegetation, elevation, and tidal inundation period. Therefore, further investigation into how community composition changes along the mosaic of habitat types within US Gulf coast estuaries is needed.

Despite the prevalence of coastal forests, research has yet to investigate nekton communities supported by different types of coastal forested shorelines, specifically the eroded-forest. Coastal forested shorelines are common along the US Gulf coast, especially in Florida with upwards of 44% of the shoreline area being this habitat type between Pensacola Bay and Southern Big Bend in Florida, USA (Geselbracht et al., 2015). Even with the understudied nature of coastal forests, they have been recognized to provide ecosystem services, such as effective flood prevention habitats. For example, the construction of the Mississippi River Gulf Outlet required significant loss of coastal forests in Breton Sound, Louisiana and is thought to be a contributing factor to exacerbated flooding during Hurricane Katrina (Kemp, 2008; Shaffer et al., 2009; Van Heerden et al., 2009). Another benefit provided by coastal forests, compared to marshes, is that they buffer wind generated waves and surges more effectively (Kemp, 2008; Shaffer et al., 2009). Evidence from palustrine forested wetlands suggests that forested shorelines may contribute to nutrient removal (Engle, 2011), but these systems lack tidal influence and experience much lower salinities than estuarine forests. These differences limit how well results from palustrine focused studies can be applied to estuarine settings, underscoring the need for additional research on estuarine forested wetlands. Data on nekton communities in these habitats are similarly scarce. In this study, we focus on eroded-forest shorelines, coastal forests that have been eroded over time, exposing roots and falling trees into the surf zone. These shorelines provide structural complexity analogous to mangroves, which similarly create tidally exposed microhabitats through high interstitial spaces (Vorsatz et al., 2021). These microhabitats in mangroves are known to provide shelter against predation and support diverse nekton communities (Aguilera et al., 2014; Guedes et al., 2023). These similarities underscore the need to understand how eroded-forest shorelines provide habitat benefits for nekton.

Although beaches, marshes, and eroded-forested shorelines are all common along the northern Gulf coast, the nekton communities they support are likely shaped by distinct habitat characteristics. Given these differences, nekton communities may vary across shoreline types, yet all three habitats provide nursery and refuge functions, suggesting that some overlap in community composition should also be expected. Understanding the balance between shared functions and habitat-specific differences is critical for predicting how shoreline restoration may shape estuarine biodiversity and the quality of habitat available to nekton communities. To address these knowledge gaps and inform future shoreline management, this study is focused on assessing nekton species richness and diversity communities along eroded-forest, marsh, and beach estuarine shorelines within East Bay, Panama City, Florida,

USA. The other objective for this study is to identify trends in community characteristics among different shoreline types. We hypothesized that eroded-forest and marsh shorelines would support similar levels of nekton abundance and diversity, both exceeding those of beach shorelines due to greater habitat complexity. Results of this study could be used to inform shoreline management and protection prioritization and planning throughout the northern US Gulf coast.

2. Methods

2.1. Study site

Study sites were located within the Florida Panhandle in East Bay (Fig. 1). East Bay is in Bay County Florida, extending southeast of the DuPont Bridge covering 7551 ha (Brim and Handley, 2003) and situated between extensive residential development to the northwest and Tyndall Air Force Base, which stretches almost the entire southern shoreline (Fig. 1). Sandy and Wetappo creek enter East Bay at the eastern end, creating a slight salinity gradient from eastern (lower) to western (higher). However, average salinity across the bay typically ranges from 17.03 to 37.73 ppt, with an average of 32.05 ppt during the study period (National Water Quality Monitoring Council). Fairly stable seagrass ecosystems cover East Bay with 660 ha of continuous-type coverage documented in 1992 (Brim and Handley, 2003). Marsh, beach, and eroded-forest shoreline types are common throughout the Bay.

2.2. Site selection

The southern (relatively undeveloped) shoreline of East Bay (Florida, USA) was scouted to identify 9 sites for this study, grouped into 3 blocks (Fig. 1). Each block contained an eroded-forest, marsh, and beach site (Fig. 2). Eroded-forest sites were characterized by scoured shoreline with trees and brush located at higher elevation and a minimum of 0.5 m drop between the tree line and low water line (Fig. 2a). These sites commonly consisted of tidally inundated fallen trees, steep shoreline drops up to 1.5 m, and canopy coverage from existing tree lines. Lower portions of scarp were accessible to nekton over a tidal cycle. Salt marsh sites consisted of a typical salt marsh shoreline that experienced tidal inundation, a slight elevation gradient, and composed of *Juncus roemerianus* and *Spartina* species (Fig. 2b). Beach sites lacked a sharp drop in elevation, exhibiting more gradual gradient slopes from the vegetation line to the waterline (Fig. 2c). At each selected site, a 60 m long stretch of shoreline was marked on the ends with PVC poles and used for all subsequent sampling.

2.3. Nekton sampling

Sampling was conducted at all sites during the same period (within 5 days of the New Moon period) and tidal stages (high tide) over the course of four seasons represented as May, July, and October 2023, and February 2024.

Nylon seine nets measuring up to 10m length and 2m depth with a ¼" (0.635 cm) stretch mesh size and 2 m × 2 m X 2 m bag were pulled parallel to the shoreline in pairs simultaneously for 20 m with one seine sampling as near the shoreline as possible and another 20 m-30 m away from the shoreline. These seine pulls were conducted at either end of the 60 m long shoreline site, leaving a 20 m unsampled gap between seine pulls (Fig. 3). At the end of each 20 m seine pull, the net was closed to capture nekton. Nekton captured were identified to species on site, counted, and total length measured for 10 individuals of each species prior to release.

2.4. Data analysis

Community composition was assessed through counts (used a proxy for abundance), Shannon diversity, and species richness metrics to
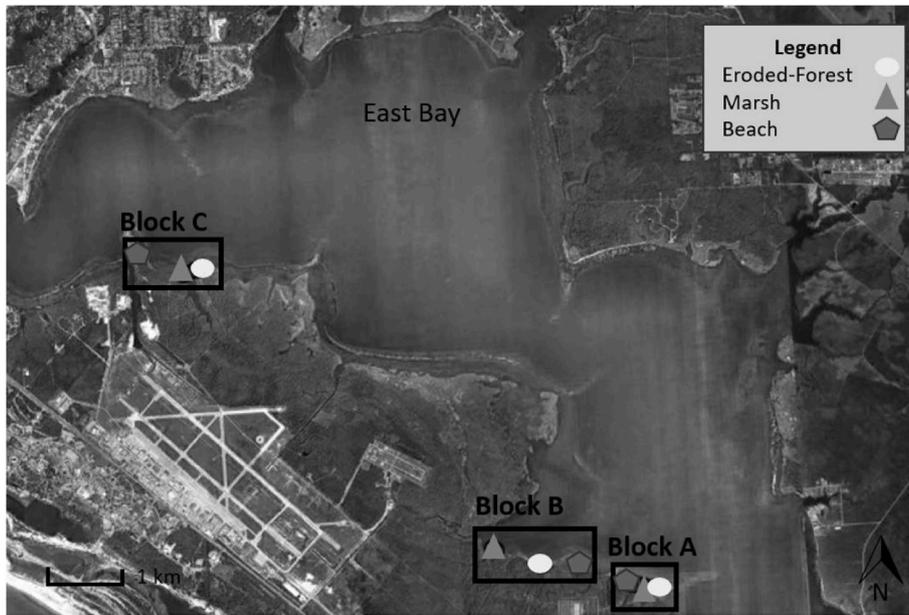
Fig. 1. Map of the study area in East Bay, Panama City, FL, USA depicting all 9 sites arranged in three blocks, each block containing one of each shoreline type. Circles represent eroded-forests, triangles represent marsh sites, and pentagons represent beach sites.

Fig. 2. Shoreline types used during the study include eroded-forest (2a), marsh (2b), and beach (2c).
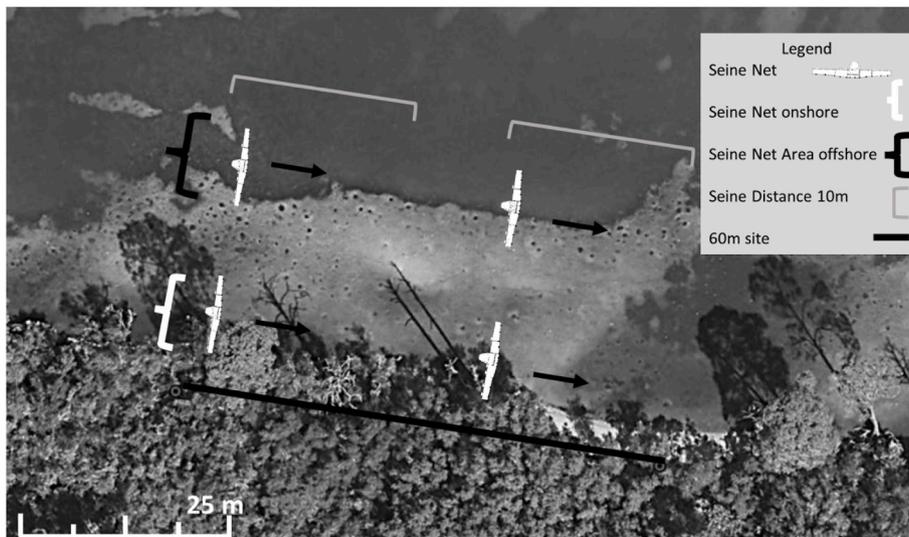

Fig. 3. Demonstration of sampling to occur at one 60m site. Seine nets were paired so that one samples nearest the shoreline and another just offshore. Seines were pulled parallel to the shoreline at 0-20m and 40-60m at each site.

determine associations between shoreline type and nekton communities over the entire study period and within seasons. For each site and season, two seine pulls were conducted at each position (onshore and offshore). Counts from the two pulls were summed to produce a single observation per position per site per season. These summed values were then used to calculate total abundance, species richness, and Shannon diversity. Consequently, each row in the statistical models represents an independent site × position × season observation (N = 72), and individual seine pulls were not treated as separate observations, avoiding pseudo-replication. All statistical analyses were conducted in R (version

4.3.1; R Core Team, 2024) using RStudio (version 2023.09.1). To examine differences in community structure, we applied quarter root transformations to abundance data to reduce the influence of dominant species and improve homogeneity of variance and residual structure and were then analyzed using a linear model with Gaussian error distributions. Quarter root transformation has been used in nekton community studies before as an acceptable method for reducing overrepresentation of species with high catch number (Silva et al., 2011; Sobrino et al., 2012; Weible et al., 2021). Non-Metric Multidimensional Scaling (NMDS) based on the Bray-Curtis dissimilarity index was performed with the vegan package (version 2.7.9; Oksanen, 2015) on transformed data to visualize patterns in nekton community composition across different seasons overall and across seasons for each shoreline type. Shannon-Weiner Diversity Index, which incorporates both species richness and evenness of their relative abundance, was used to calculate diversities within each sampling site for all shoreline types and analyzed using a linear model. Species richness was analyzed using generalized linear models with a Poisson error distribution and log link. All models included block, position, sampling event, shoreline type, and their interaction as fixed effects (R equation $\sim$ block + position + sampling event + shoreline type + sampling event: shoreline type). Model assumptions were assessed using residual diagnostics using the performance (version 0.15.0; Lüdecke et al., 2021) and DHARMa (version 0.4.7; Hartig, 2024) packages, visual inspection of distributions, and a transformation (quarter root transformed abundance data) was applied where necessary to meet model assumptions. Post hoc pairwise comparisons among seasons and among shoreline types were conducted using estimated marginal means with emmeans (version 1.11.2; Lenth, 2025). Pairwise p-values were Tukey-adjusted to account for multiple comparisons. Statistical significance was assessed at $p < 0.05$.

3. Results

Over the course of the study, a total of 5894 individual nekton were collected. The five most abundant species were pinfish (*Lagodon rhomboides*, n = 1423), shrimp species (*Caridea spp.*, n = 993), spot (*Leiostomus xanthurus*, n = 894), bay anchovy (*Anchoa mitchilli*, n = 716), and inland silverside (*Menidia beryllina*, n = 712). These species together accounted for 80.4% of the total nekton captured during the study (Table 1; see Table S1 for mean abundances by species, shoreline type, and season).

Visualization of community composition using non-metric multidimensional scaling (NMDS) revealed seasonal variation in nekton communities, with clear clustering by season and greater dispersion in winter (Fig. 4). In the paneled NMDS plot (Fig. 5), points were distinguished by shoreline type within each season. Fall exhibited the largest 95% confidence ellipse, indicating the greatest variability in community composition among sites, while spring, summer, and winter showed tighter clustering, suggesting lower dispersion in nekton assemblages across these seasons.

To statistically test differences in community composition metrics, we conducted separate linear models for total abundance, species richness, and Shannon diversity (Table 2). Effect sizes for these main effects are reported in Table 2: partial η^2 for abundance and Shannon diversity, and incidence rate ratios with 95% confidence intervals for richness. Neither block nor position significantly influenced abundance or Shannon diversity (p > 0.05), but position was slightly significant on species richness (p = 0.0432). However, season had a significant effect on both species richness ($\chi^2 = 20.509$, p = 0.0001) and Shannon diversity (F = 5.084, p = 0.0035), but not total abundance (F = 1.666, p = 0.1844). Likewise, shoreline type significantly influenced species richness ($\chi^2 = 12.634$, p = 0.0018) and Shannon diversity (F = 3.948, p = 0.0248), but not abundance (F = 1.808, p = 0.1733). No significant interaction was found between season and shoreline type for any metric.

Post hoc pairwise comparisons using estimated marginal means revealed that species richness was significantly lower in spring than in

Table 1

Nekton species caught during study period in East Bay, Panama City, Florida organized by family with the quantity of individuals caught during the study. Dietary preferences and scientific names validated using the online database FishBase (Froese and Pauly, 2000; Sa-a et al., 2000).

Family	Scientific name	Common name	Dietary Preference	Quantity
Achiridae				
	Trinectes maculatus	Hogchoker	Invertebrates, worms	7
Atherinopsidae				
	Menidia beryllina	Inland silverside	Algae, small invertebrates	712
	Menidia peninsulae	Tidewater silverside	Algae, small invertebrates	2
Belonidae				
	Strongylura marina	Atlantic needlefish	Invertebrates, fishes	1
	Strongylura notata	Redfin needlefish	Invertebrates, fishes	12
	Tylosurus rafale	Atlantic aguijon	Invertebrates, fishes	1
Blenniidae				
	Chasmodes bosquianus	Striped blenny	Invertebrates, fishes	13
	Unknown	Unknown blenny sp.		7
Caridea				
	Caridea sp.	Shrimp spp.	Detritivore	993
Cyprinodontidae				
	Cyprinodon variegatus variegatus	Sheepshead minnow	Algae, fish, insects, detritus	21
Dasyatidae				
	Dasyatis sabina	Atlantic stingray	Invertebrates, fishes	2
Engraulidae				
	Anchoa mitchilli	Bay Anchovy	Zooplankton	716
Fundulidae				
	Adinia xenica	Diamond killifish	Algae, insect larvae	12
	Fundulus grandis	Gulf killifish	Fishes, insects, algae	3
	Fundulus heteroclitus	Mummichog	Detritus, insects, crustacea, fish	30
	Fundulus similis	Longnose killifish	Zooplankton, algae, crustacea	80
	Lucania parva	Rainwater killifish	Crustacea and insect larvae, invertebrates	99
Gerreidae				
	Eucinostomus harengulus	Tidewater mojarra	Invertebrates	237
Gobiidae				
	Bathygobius soporator	Frillfin goby	Algae, invertebrates	30
	Ctenogobius boleosoma	Darter goby	Algae, invertebrates	2
	Evorthodus lyricus	Lyre goby	Algae, invertebrates	1
	Lophogobius cyprinoides	Crested goby	Algae, invertebrates	2
Haemulidae				
	Orthopristis chrysoptera	Pigfish	Invertebrates, fishes	61
Leiostomus				
	Leiostomus xanthurus	Spot	Invertebrates, detritus	894
Lobotidae				
	Lobotes surinamensis	Atlantic tripletail	Invertebrates, fishes	1
Lutjanidae				
	Lutjanus griseus	Gray snapper	Fishes, invertebrates, plankton	3
Mugilidae				
	Mugil cephalus	Mullet	Algae, plankton	1
Panopeidae				
	Panopeus obesus	Mud crab	Mollusks, fishes	7
Paralichthyidae				

Table 1 (*continued*)

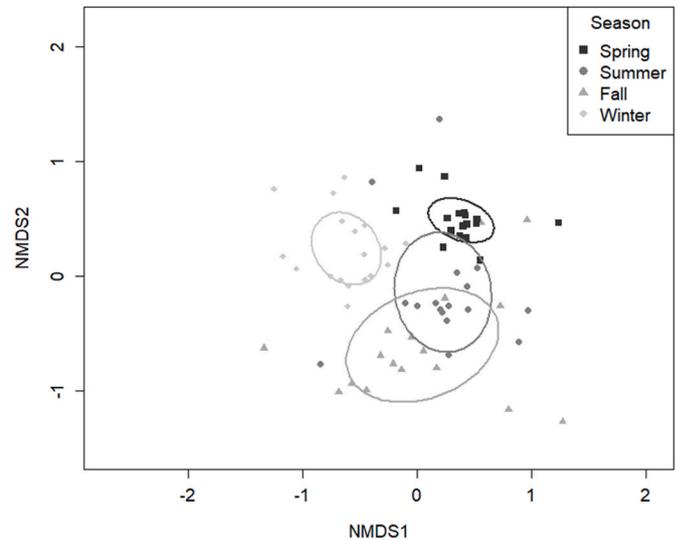| Family	Scientific name	Common name	Dietary Preference	Quantity
	Paralichthys albiguttata	Gulf flounder	Crustacea, fishes	4
	Paralichthys lethostigma	Southern flounder	Crustacea, fishes	1
Poeciliidae				
	Poecilia latipinna	Sailfin molly	Algae, insects, copepods	3
Portunidae				
	Callinectes sapidus	Blue crab	Mollusks fishes	44
Sciaenidae				
	Cynoscion nebulosus	Spotted seatrout	Crustacea, fishes	75
	Sciaenops ocellatus	Red drum	Invertebrates, fishes	17
	Stellifer lanceolatus	Star drum	Crustacea	291
Sparidae				
	Lagodon rhomboides	Pinfish	Crustacea, fishes	1423
Syngnathidae				
	Hippocampus zosterae	Dwarf seahorse	Crustacea, fishes	1
	Microphis brachyurus lineatus	Opossum pipefish	Crustacea	5
	Syngnathus fuscus	Northern pipefish	Crustacea	13
	Syngnathus louisianae	Chain pipefish	Crustacea	11
	Syngnathus scovelli	Gulf pipefish	Crustacea	21
Synodontidae				
	Synodus foetens	Inshore lizardfish	Fishes, crustacea	1
Terapontidae				
	Bairdiella chrysoura	Silver perch	Crustacea, fishes	29
Tetraodontidae				
	Sphoeroides maculatus	Northern puffer	Invertebrates, fishes	2
	Sphoeroides nephelus	Southern puffer	Invertebrates, fishes	3

Fig. 4. Non-Metric Multidimensional Scaling (NMDS) plot of nekton community composition during entire study period, with points colored by season, stress value of 0.181. Ellipses represent one standard deviation around the centroid grouping, illustrating the spread and clustering of nekton communities. The plot is based on Bray-Curtis dissimilarity and visualizes the separation of nekton communities across different seasons.

summer (p = 0.0005), fall (p = 0.0122), and winter (p = 0.0009) (Fig. 6 B). For Shannon diversity, spring also had significantly lower values than both summer (p = 0.0024) and winter (p = 0.0297; Fig. 6 C), with greater biodiversity during summer and winter. No other seasonal pairwise comparisons were significant (p > 0.05).

For shoreline types, marshes supported significantly higher species richness than beaches (p = 0.0013) and had significantly higher Shannon diversity than beaches (p = 0.0185; Fig. 7 B & 7 C). Differences between marshes and eroded-forests, and between beaches and eroded-forests, were not significant for Shannon diversity or richness (p > 0.05; Table 2).

4. Discussion

These results provide insights into the dynamics of nekton community composition by comparing beach, marsh, and eroded-forest shorelines in East Bay. Clear patterns emerged with nekton community composition and biodiversity being driven primarily by season and shoreline type. Seasonal shifts in recruitment and habitat use likely drove lower spring diversity relative to other seasons. Effect sizes for these patterns (Table 2) indicate that season explained a moderate portion of the variance in Shannon diversity (partial η^2 = 0.21) and corresponded to substantial changes in species richness, with Fall richness ~66% higher than Spring (IRR = 1.66, 95% CI: 1.08–2.54). These results suggest that seasonal dynamics strongly influence nekton community structure. Marsh shorelines supported more diverse assemblages

than beaches, highlighting the role of structurally complex habitats in supporting nekton diversity. Consistent with our hypothesis, shoreline habitat complexity emerged as an important driver of nekton community structure, with eroded-forest and marsh shorelines supporting comparable levels of abundance and diversity and generally exceeding those observed along beach shorelines. These findings indicate that eroded-forest shorelines function as ecologically valuable habitats and should be considered alongside marshes in shoreline management and conservation planning across the northern Gulf of Mexico. Seasonal variation in nekton community composition likely reflects a combination of ecological processes ranging from recruitment pulses and reproductive timing or migration (Ribeiro et al., 2012) to responses from resource availability (Horinouchi, 2007; Ruesink et al., 2019). Species specific seasonal migrations potentially decrease resident nekton species abundance due to introduced predation or resource competition in seagrass habitats (Kneib and Knowlton, 1995). Although only sampled over a single year in this study, the distinct community clustering observed in spring and fall suggests seasonal synchrony in life history events, such as spawning or juvenile recruitment, which may concentrate certain species during these periods (Mathieson et al., 2000; Paterson and Whitfield, 2000). In contrast, the broader spread of communities observed in Winter points to increased variability, potentially driven by abiotic factors (Peterson and Grubbs, 2023). Freshwater input from seasonal rainfall is a known influence on water quality parameters commonly influencing species composition and abundance in estuarine systems (Wellborn et al., 1996; Horinouchi, 2007; Loke and Todd, 2016). Seasonal shifts in community structure are well documented in estuarine systems, where many species use these habitats transiently, often aligning their presence with favorable environmental conditions or reproductive cycles. These dynamics help explain distinct seasonal clusters revealed by the NMDS plot (Figs. 4 and 5) and underscore the importance of capturing seasonal snapshots to accurately assess estuarine community composition and habitat use.

Although NMDS ordinations showed substantial overlap in community composition among shoreline types, diversity indices revealed significant differences in species richness and Shannon diversity. This pattern indicates that shoreline types supported broadly similar species
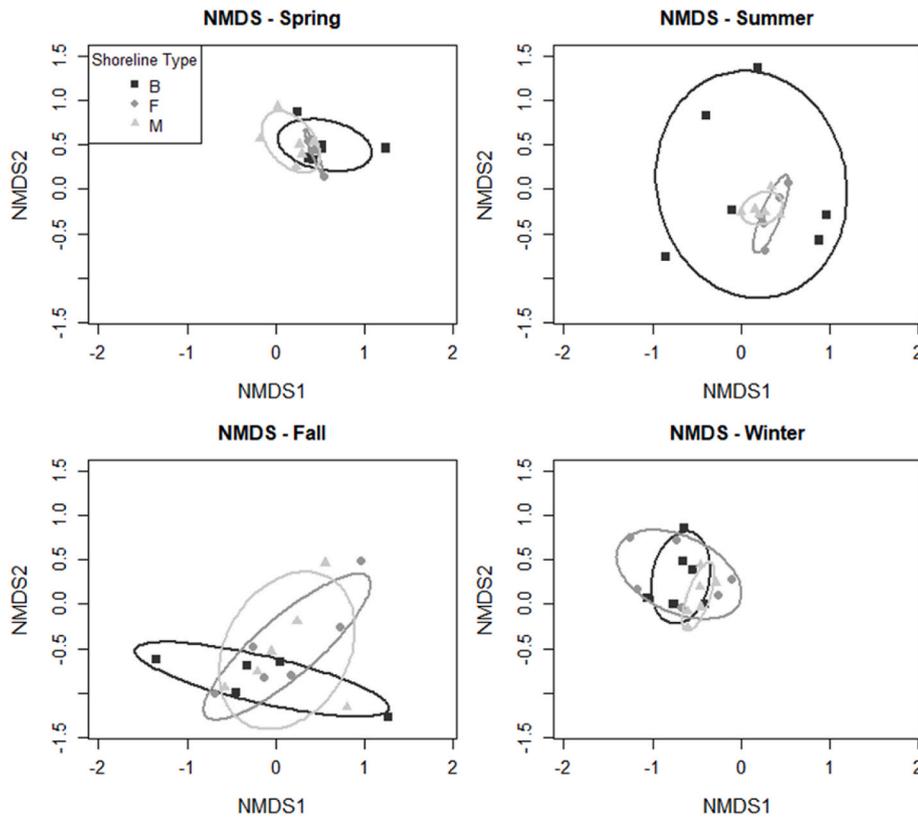
Fig. 5. Four panel plot displaying Non-Metric Multidimensional Scaling (NMDS) plots of nekton community composition with points distinguished by the shoreline B, F, M (beach, eroded-forest, marsh respectively) within each season, stress value 0.181. Ellipses represent one standard deviation around the centroid grouping, illustrating the spread and clustering of nekton communities. The plot is based on Bray-Curtis dissimilarity and visualizes the separation of fish communities across different shoreline types and seasons.

Table 2
Separate model results for nekton abundance (lm), richness (Poisson GLM), and Shannon Diversity (lm), including partial η^2 (95% CI) for main effects. The bottom section shows significant pairwise comparisons for richness and Shannon Diversity based on Estimated Marginal Means post hoc tests, including effect sizes (Incidence Rate Ratios (IRR) for richness, mean differences for Shannon diversity) with 95% confidence intervals. For the top table, block refers to the grouping of sites, position is seine pulled adjacent to the shoreline and 20-30 offshore, type is shoreline type (eroded-forest, marsh, or beach), and season is winter, spring, summer, or fall sampling.

Factor	Abundance				Richness		Shannon Diversity		
	Df	F	p- value	η^2 (95% CI)	χ^2	p-value	F	p-value	η^2 (95% CI)
Block	2	0.645	0.5285	0.02 [0.0,1.0]	0.465	0.7925	0.036	0.9647	0.001 [0.0,1.0]
Position	1	2.170	0.1462	0.04 [0.0,1.0]	4.089	**0.0432***	2.275	0.1370	0.04 [0.0,1.0]
Season	3	1.666	0.1844	0.08 [0.0,1.0]	20.509	**0.0001***	5.084	**0.0035****	0.21 [0.05,1.0]
Type	2	1.808	0.1733	0.06 [0.0,1.0]	12.634	**0.0018***	3.948	**0.0248***	0.12 [0.01,1.0]
Season × Type	6	0.693	0.6564	0.07 [0.0,1.0]	4.436	0.6179	0.366	0.8973	0.04 [0.0,1.0]

Pairwise Estimated Marginal Means Post Hoc	Richness				Shannon Diversity		
Factor	IRR	p-value	95% CI	Mean difference	p-value	95% CI	
Fall vs Spring	1.660	**0.0122***	1.083 – 2.542	0.347	0.1449	−0.077 - 0.770	
Fall vs Summer	0.877	0.7825	0.613 – 1.254	−0.251	0.4050	−0.674 - 0.173	
Fall vs Winter	0.899	0.8709	0.629 – 1.286	−0.110	0.9012	−0.533 – 0.313	
Spring vs Summer	0.528	**0.0005****	0.348 – 0.802	−0.597	**0.0024***	−1.020 to −0.174	
Spring vs Winter	0.542	**0.0009****	0.357 – 0.822	−0.457	**0.0297***	−0.880 to −0.033	
Summer vs Winter	1.025	0.9978	0.725 – 1.449	0.141	0.8155	−0.283 – 0.564	
Beach vs Eroded-Forest	0.826	0.3523	0.597 – 1.143	−0.175	0.4228	−0.508 – 0.159	
Beach vs Marsh	0.632	**0.0013***	0.465 – 0.859	−0.388	**0.0185***	−0.722 to −0.055	
Eroded-Forest vs Marsh	0.765	0.0752	0.574 – 1.021	−0.214	0.2783	−0.547 – 0.119	

Significance denoted as * p < 0.05 **p < 0.01 ***p < 0.001.

assemblages but differed in the distribution and evenness of taxa, highlighting the complementary information provided by multivariate and univariate approaches. Our findings indicate that marshes supported significantly higher species richness and Shannon diversity than beaches, but generally higher than eroded-forest shorelines as well (Fig. 7). Shoreline type influenced nekton biodiversity, with marshes

supporting higher species richness and Shannon diversity than beaches. Species richness was significantly lower in beaches compared to marshes (IRR = 0.632, 95% CI: 0.465–0.859), while Shannon diversity was lower in beaches by 0.388 units (95% CI: 0.722 to −0.055), emphasizing the ecological importance of structurally complex marsh habitats. This pattern may be attributed to several ecological factors that make
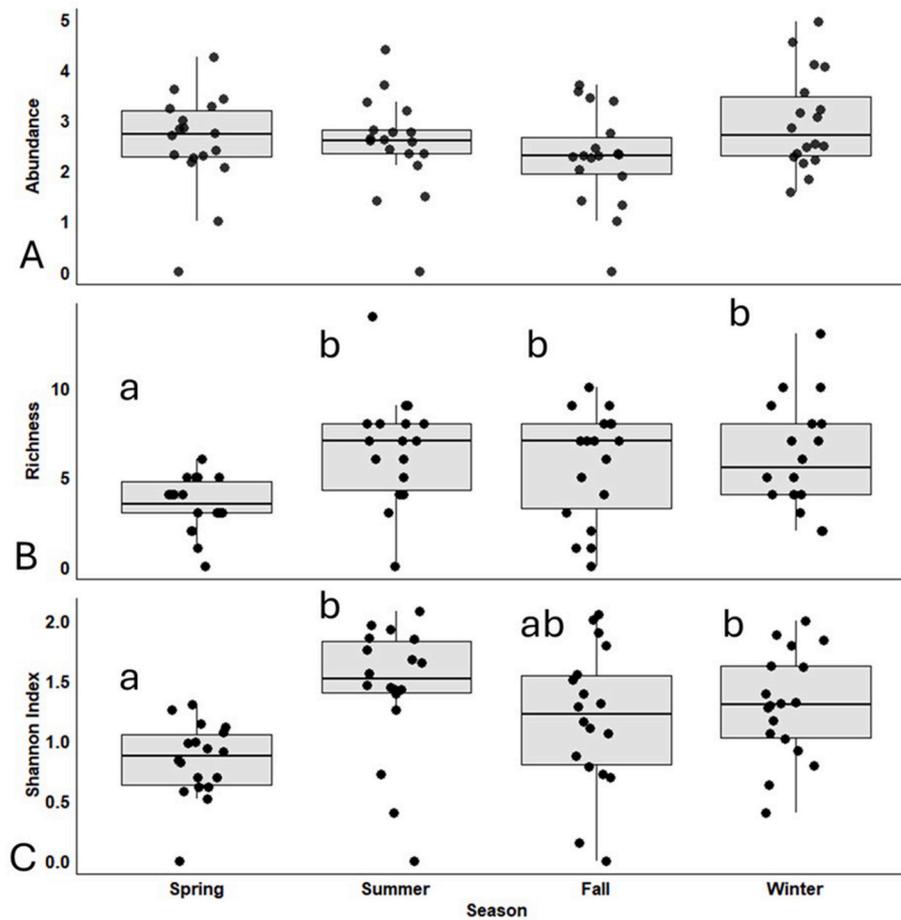
Fig. 6. Box plots showing the interquartile range with overlaid points showing (A) quarter root-transformed abundance, (B) species richness, and (C) Shannon diversity across seasons (Spring, Summer, Fall, Winter), pooled across all shoreline types. Different lowercase letters above boxplots indicate significant differences based on Estimated Marginal Means (EMMs) pairwise post-hoc tests (p < 0.05).

marshes suitable habitats for a greater variety of nekton. Marshes often provide more complex habitat structures, such as dense vegetation and a variety of microhabitats, which can support a greater diversity of species (Judd and Lonard, 2002). Additionally, marshes are highly productive ecosystems, offering abundant food resources and refuge for juvenile nekton (Rocha and Goulden, 2009; Sousa et al., 2010). The higher productivity and structural complexity of marsh habitats contribute to greater species richness and evenness, as these conditions support a wider range of species at various life stages, including both resident and transient species (Judd and Lonard, 2002; Rocha and Goulden, 2009).

Seasonal variation also strongly influenced nekton biodiversity. Species richness was significantly lower in spring compared to summer (IRR = 0.528, 95% CI: 0.348–0.802) and winter (IRR = 0.542, 95% CI: 0.357–0.822), while Shannon diversity was lower in spring relative to summer (−0.597, 95% CI: 1.020 to −0.174) and winter (−0.457, 95% CI: 0.880 to −0.033). These effect sizes indicate that the magnitude of seasonal differences is substantial, highlighting the ecological relevance of temporal dynamics in structuring nekton communities. The magnitude and pattern of nekton association with different shoreline types varied by season. According to disturbance theory, habitats experiencing intermediate levels of disturbance can support higher biodiversity by preventing competitive exclusion (Connell, 1978). Marsh and eroded-forest shorelines may experience moderate seasonal physical disturbance (e.g., from tidal flow or detritus accumulation), which can directly influence nekton by altering shelter, foraging opportunities, or access to microhabitats, thereby maintaining a dynamic but diverse community. Modifications to tidal flow have been documented to alter

patterns of nekton distribution and abundance in salt marshes (Olin et al., 2015). Beaches tend to have a homogenized habitat but can still experience seasonal disturbances from storm wave events and rainfall, both documented to impact macrofaunal richness of beaches seasonally (Costa et al., 2019). These seasonal-habitat interactions emphasize that biodiversity patterns in estuarine systems are not static but fluctuate in response to ecological processes that are both temporally and spatially variable.

In addition to seasonal and shoreline-specific patterns, the widespread presence of submerged aquatic vegetation (SAV) throughout the bay may have contributed to habitat redundancy, potentially dampening the differences observed among shoreline types. SAV provides structurally complex habitat that supports foraging, refuge, and nursery functions for a variety of nekton species, often rivaling or complementing the ecological roles of shoreline habitats (McDonald et al., 2016). When SAV is abundant and broadly distributed, nekton may not rely solely on shoreline features for habitat, which can buffer differences in species composition or abundance across shoreline types. This functional redundancy may help explain the lack of more pronounced differences in nekton biodiversity between shoreline types in certain seasons because SAV biomass changes seasonally as well. Ultimately, these patterns underscore the importance of considering habitat mosaics in estuarine systems, where nekton utilize a combination of habitat types across the landscape rather than being restricted to one dominant feature.

Limitations of this study exist within the temporal and spatial scope. Sampling was conducted over a single year, which may not capture
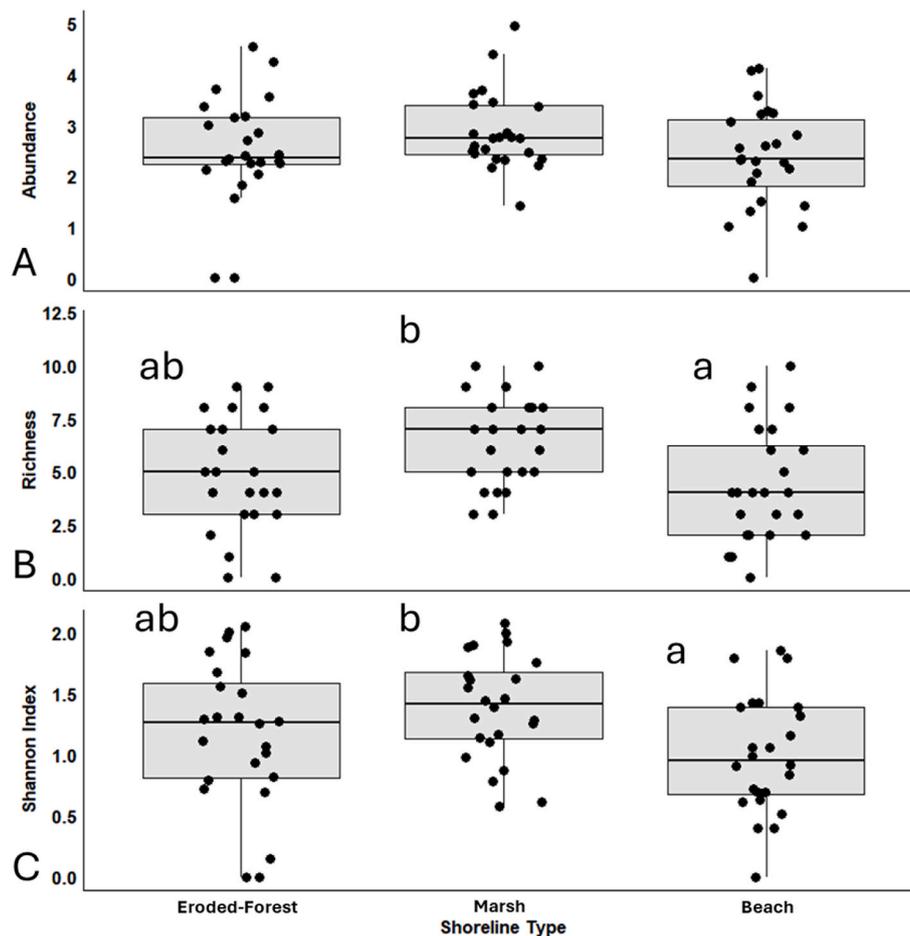
Fig. 7. Box plots showing the interquartile range with overlaid points showing (A) quarter root-transformed abundance, (B) species richness, and (C) Shannon diversity across shoreline types (Eroded-Forest, Marsh, Beach), pooled across all seasons. Different lowercase letters above boxplots indicate significant differences based on Estimated Marginal Means (EMMs) pairwise post-hoc tests ($p < 0.05$).

interannual variability in nekton community dynamics due to natural fluctuations in environmental conditions such as temperature, salinity, and freshwater inflow. Additionally, the study design included only three spatial blocks, each containing one site per shoreline type, for a total of nine sites. While this design allowed for standardized comparisons and was feasible for the project team to complete within a reasonable timeframe (same day and portion of tidal cycle) within each sampling period, it constrained the statistical power and generalizability of the findings across broader geographic areas or estuarine systems. Eroded-forest shorelines sampled during this study proved difficult to seine due to tree roots, fallen trees, and oyster growth on fallen trees that would all contribute to snags in seine nets. In contrast, the more simplified habitats of beaches may provide fewer resources and less structural complexity, which could explain the lower species richness and Shannon diversity observed in these areas (Gibson et al., 1993; Rodrigues and Vieira, 2013). Interestingly, while species richness and diversity were significantly greater in marshes compared to beaches, no significant differences in nekton abundance were observed across shoreline types, which may be attributed to the sampling design and scale of this study (Fig. 7 A). Within East Bay, it was difficult to identify more blocks with all three shoreline types as beaches were limiting, that also exhibited a consistent presence of submerged aquatic vegetation. Future studies should aim to extend sampling over multiple years to capture longer-term trends and account for potential anomalies in seasonal patterns. Future studies should also incorporate areas with and without SAV to further parse out shoreline type influence in the absence of alternative habitats (SAV). Increasing the number of blocks, therefore

incorporating a greater number of replicate sites per shoreline type, would also enhance the robustness of statistical analyses and help disentangle site-specific effects from broader habitat trends.

These findings have important implications for coastal conservation and habitat management. Our results show that eroded-forest shoreline habitats support biodiversity levels comparable to beaches but do not consistently exceed those of marshes. This is one of the first studies that evaluated eroded-forest shorelines in estuaries and one of many for marshes showing that these structurally complex environments contribute to estuarine habitat heterogeneity and ecological value. This underscores the importance of conserving or restoring a mosaic of shoreline types within estuarine systems. A diverse mosaic of habitats, eroded-forests, marshes, and beaches, supports different components of the nekton community across seasons, likely reflecting species-specific habitat needs during recruitment, foraging, and refuge-seeking behaviors. Management efforts that prioritize maintaining or restoring a heterogeneous shoreline landscape are more likely to sustain robust and resilient nekton communities throughout the year. As estuarine environments continue to face pressures from development, erosion, and sea level rise, protecting this habitat diversity becomes increasingly critical for sustaining fisheries and ecosystem function.

CRediT authorship contribution statement

Cynthia Lupton: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **J. Marcus Drymon:**

Writing – review & editing, Supervision. **Mark Woodrey:** Writing – review & editing, Supervision. **Nigel Temple:** Writing – review & editing, Supervision. **Steven Scyphers:** Writing – review & editing, Supervision. **Eric Sparks:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Conceptualization.

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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.marenvres.2026.107925.

Data availability

Data will be made available on request.

References

Able, K.W., Wuenschel, M.J., Grothues, T.M., Vasslides, J.M., Rowe, P.M., 2013. Do surf zones in New Jersey provide "nursery" habitat for southern fishes? Environ. Biol. Fish. 96 (5), 661–675.

Aguilera, M.A., Broitman, B.R., Thiel, M., 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. Mar. Pollut. Bull. 87 (1-2), 257–268.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51 (8), 633–641.

Brim, M.S., Handley, L.R., 2003. St. Andrew Bay. Seagrass Status and Trends in the Northern Gulf of Mexico, pp. 155–169.

Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. Glob. Biogeochem. Cycles 17 (44), 1–22.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. Science 199 (4335), 1302–1310.

Costa, L.L., Machado, P.M., Zalmon, I.R., 2019. Do natural disturbances have significant effects on sandy beach macrofauna of Southeastern Brazil? Zool. 36, e29814.

Engle, V.D., 2011. Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. Wetlands 31 (1), 179–193.

Froese and D. Pauly (eds.) Fishbase 2000: Concepts, Design and Data Sources. ICLARM, Los Baños, Laguna, Philippines. 344 p.

Geselbracht, L.L., Freeman, K., Birch, A.P., Brenner, J., Gordon, D.R., 2015. Modeled sea level rise impacts on coastal ecosystems at six major estuaries on Florida's gulf coast: implications for adaptation planning. PLoS One 10 (7), e0132079.

Gibson, R.N., Ansell, A.D., Robb, L., 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 89–105.

Gittman, R.K., Fodrie, F.J., Popowich, A.M., Keller, D.A., Bruno, J.F., Currin, C.A., Peterson, C.H., Piehler, M.F., 2015. Engineering away our natural defenses: an analysis of shoreline hardening in the US. Front. Ecol. Environ. 13 (6), 301–307.

Glover, K.M., Kimball, M.E., Pfirrmann, B.W., Pelton, M.M., Dunn, R.P., 2023. Juvenile brown shrimp (farfantepenaeus aztecus) use of salt marsh intertidal creeks as nursery habitat. Estuaries Coasts 46 (7), 1895–1906.

Guedes, É., Pereira, J., Brito, G., Pessanha, A., Júnior, A., 2023. Predation Risk, Foraging and Reproduction of an Insectivore Fish Species Associated with Two Estuarine Habitats.

Hackney, C.T., Posey, M.H., Ross, S.W., Norris, A.R., 1996. A Review and Synthesis of Data on Surf Zone Fishes and Invertebrates in the South Atlantic Bight and the Potential Impacts from Beach Renourishment. US Army Corps of Engineers, Wilmington, NC. Technical Report.

Hartig, F., 2024. _DHARMa: residual diagnostics for hierarchical (Multi-Level/mixed) regression models_. R package version 0.4.

Horinouchi, M., 2007. Review of the effects of within-patch scale structural complexity on seagrass fishes. J. Exp. Mar. Biol. Ecol. 350 (1-2), 111–129.

Judd, F.W., Lonard, R.I., 2002. Species richness and diversity of brackish and salt marshes in the Rio Grande Delta. J. Coast Res. 751–759.

Kemp, G.P., 2008. Mississippi River Gulf outlet effects of storm surge, waves, and flooding during Hurricane Katrina. Expert Report 4.

King, S.E., Lester, J.N., 1995. The value of salt marsh as a sea defence. Mar. Pollut. Bull. 30 (3), 180–189.

Kneib, R.T., Knowlton, M.K., 1995. Stage-structured interactions between seasonal and permanent residents of an estuarine nekton community. Oecologia 103, 425–434.

Ledford, T.C., Mortazavi, B., Tatariw, C., Starr, S.F., Smyth, E., Wood, A.G., Simpson, L. T., Cherry, J.A., 2021. Ecosystem carbon exchange and nitrogen removal rates in two 33-year-old constructed salt marshes are similar to those in a nearby natural marsh. Restor. Ecol. 29 (7), e13439.

Lenth, R., 2025. _emmeans: estimated marginal means, aka least-squares means_. R package version 1.11.2. https://CRAN.R-project.org/package=emmeans.

Loke, L.H., Todd, P.A., 2016. Structural complexity and component type increase intertidal biodiversity independently of area. Ecology 97 (2), 383–393.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6 (60), 3139. https://doi.org/10.21105/joss.03139.

Mathieson, S., Cattrijsse, A., Costa, M.J., Drake, P., Elliott, M., Gardner, J., Marchand, J., 2000. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar. Ecol. Prog. Ser. 204, 225–242.

McDonald, R.B., Moody, R.M., Heck, K.L., Cebrian, J., 2016. Fish, macroinvertebrate and epifaunal communities in shallow coastal lagoons with varying seagrass cover of the northern Gulf of Mexico. Estuaries Coasts 39, 718–730.

National Water Quality Monitoring Council, 2025. Water quality portal. hyperlink_for_query. https://doi.org/10.5066/P9QRKUVJ. (Accessed 5 December 2025).

Oksanen, J., 2015. Vegan: community ecology package. R package version 2, 3.

Olds, A.D., Vargas-Fonseca, E., Connolly, R.M., Gilby, B.L., Huijbers, C.M., Hyndes, G.A., Layman, C.A., Whitfield, A.K., Schlacher, T.A., 2018. The ecology of fish in the surf zones of ocean beaches: a global review. Fish Fish. 19 (1), 78–89.

Olin, J.A., Stevens, P.W., Rush, S.A., Hussey, N.E., Fisk, A.T., 2015. Loss of seasonal variability in nekton community structure in a tidal river: evidence for homogenization in a flow-altered system. Hydrobiologia 744 (1), 271–286.

Paterson, A.W., Whitfield, A.K., 2000. Do shallow-water habitats function as refugia for juvenile fishes? Estuar. Coast Shelf Sci. 51 (3), 359–364.

Peterson, C.T., Grubbs, R.D., 2023. Temporal community structure and seasonal climatic migration of coastal sharks and large teleost fishes in the northeast Gulf of Mexico. Can. J. Fish. Aquat. Sci. 80 (8), 1335–1350.

Peterson, G.W., Turner, R.E., 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17, 235–262.

R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Available at:, Version 4.3.1. https://www.R-project.org/.

Ribeiro, J., Carvalho, G.M., Gonçalves, J.M., Erzini, K., 2012. Fish assemblages of shallow intertidal habitats of the Ria Formosa lagoon (South Portugal): influence of habitat and season. Mar. Ecol. Prog. Ser. 446, 259–273.

Rocha, A.V., Goulden, M.L., 2009. Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a Typha marsh. Agric. For. Meteorol. 149 (1), 159–168.

Rodrigues, F.L., Vieira, J.P., 2013. Surf zone fish abundance and diversity at two sandy beaches separated by long rocky jetties. J. Mar. Biol. Assoc. U. K. 93 (4), 867–875.

Ross, S.W., Lancaster, J.E., 2002. Movements and site fidelity of two juvenile fish species using surf zone nursery habitats along the southeastern North Carolina coast. Environ. Biol. Fish. 63 (2), 161–172.

Ruesink, J.L., Gross, C., Pruitt, C., Trimble, A.C., Donoghue, C., 2019. Habitat structure influences the seasonality of nekton in seagrass. Mar. Biol. 166, 1–14.

Sa-a, P., Palomares, M.L., Pauly, D., 2000. The FOOD ITEMS Table. R, pp. 182–188.

Shaffer, G.P., Day, J.W., Mack, S., Kemp, G.P., van Heerden, I., Poirrier, M.A., Westphal, K.A., FitzGerald, D., Milanes, A., Morris, C.A., Bea, R., 2009. The MRGO

navigation project: a massive human-induced environmental, economic, and storm disaster. J. Coast Res. (10054), 206–224.

Silva, L., Vila, Y., Torres, M.Á., Sobrino, I., Acosta, J.J., 2011. Cephalopod assemblages, abundance and species distribution inthe Gulf of Cadiz (SW Spain). Aquat. Living Resour. 24 (1), 13–26.

Sobrino, I., González, J., Hernández-González, C.L., Balguerias, E., 2012. Distribution and relative abundance of main species of grenadiers (Macrouridae, Gadiformes) from the African Atlantic coast. J. Ichthyol. 52 (10), 690–699.

Sousa, A.I., Lillebø, A.I., Pardal, M.A., Caçador, I., 2010. Productivity and nutrient cycling in salt marshes: contribution to ecosystem health. Estuar. Coast Shelf Sci. 87 (4), 640–646.

Stamp, T., West, E., Robbins, T., Plenty, S., Sheehan, E., 2022. Large-scale historic habitat loss in estuaries and its implications for commercial and recreational fin fisheries. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79 (7), 1981–1991.

Stockdon, K.S.D.H.F., Sopkin, D.S.T.K.S., Sallenger, N.G.P.A.H., 2012. National Assessment of hurricane-induced Coastal Erosion Hazards: Gulf of Mexico.

Valiela, I., Cole, M.L., Mcclelland, J., Hauxwell, J., Cebrian, J., Joye, S.B., 2000. Role of salt marshes as part of coastal landscapes. Concepts and Controversies in Tidal Marsh Ecology, pp. 23–36.

Van Heerden, I.L., Kemp, G.P., Bea, R., Shaffer, G., Day, J., Morris, C., Fitzgerald, D., Milanes, A., 2009. How a navigation channel contributed to most of the flooding of New Orleans during Hurricane Katrina. Public Organ. Rev. 9 (4), 291–308.

Vorsatz, L.D., Pattrick, P., Porri, F., 2021. Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: biotic and abiotic implications at the microhabitat scale. Ecol. Indic. 121, 107154.

Weible, R.M., Rodgers, K.U.S., Friedlander, A.M., Hunter, C.L., 2021. Assessing assemblage composition of reproductively mature resource fishes at a Community Based Subsistence Fishing Area (CBSFA). Diversity 13 (3), 114.

Wellborn, G.A., Skelly, D.K., Werner, E.E., 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annu. Rev. Ecol. Systemat. 27 (1), 337–363.

zu Ermgassen, P.S., DeAngelis, B., Gair, J.R., Ermgassen, S.Z., Baker, R., Daniels, A., MacDonald, T.C., Meckley, K., Powers, S., Ribera, M., Rozas, L.P., 2021. Estimating and applying fish and invertebrate density and production enhancement from seagrass, salt marsh edge, and oyster reef nursery habitats in the Gulf of Mexico. Estuaries Coasts 44, 1588–1603.