



Oyster reefs as habitat for aquatic macrofauna in a Gulf of Mexico estuary: biotic complexity at spatial, ecological, and demographic scales

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ABSTRACT: Oysters are important marine foundation species across the world, particularly in estuaries of the Gulf of Mexico. One important function of oysters in estuaries is the provision of 3-dimensional habitat that is used by a wide range of species. In this study, the biotic diversity of mid-bay intertidal oyster reefs found in a Gulf of Mexico estuary was examined at nested ecological and demographic scales. Fishery-independent data collections made in East Matagorda Bay, Texas, USA, were used to compare community structure and diversity at mid-bay reefs to undifferentiated shoreline habitats. Despite similar diversity metrics, there were differences in community structure that were driven by differences in spatial habitat use by several common species. Below the community scale, demographic differences in spotted seatrout *Cynoscion nebulosus* habitat use were observed, with smaller and younger individuals found along reefs, and larger and older individuals found along shorelines. This finding was more pronounced for male spotted seatrout in the spring. The observed spatial habitat use patterns at nested ecological scales (community, interspecies, intra-species) highlight the importance of oyster reefs for maintaining diversity in Gulf of Mexico estuaries, and more broadly support the notion that heterogeneity in localized habitats drives biotic diversity at the estuary scale. Conservation of oyster reefs as critical habitat should be considered along with conservation of oysters themselves when balancing the ecological value of oysters against the commercial value of oyster fisheries.

KEY WORDS: Oysters · Habitat · Diversity · Community structure · Gulf of Mexico · Estuaries

1. INTRODUCTION

Heterogeneity in estuarine community structure can be driven by the presence of habitat features that vary in time and space (Yáñez-Arancibia et al. 1988, Clarkson & Beseres Pollack 2021, 2022). For instance, in the northern Gulf of Mexico, oyster reefs are ubiquitous but patchily distributed estuarine benthic features that provide critical habitat for a wide range of species and promote biodiversity (Stunz et al. 2010, De Santiago et al. 2019, La Peyre et al. 2019). One of the most important functions of oyster reefs is the

provision of 3-dimensional habitat and vertical relief, which have been shown to be critical for the preservation of faunal diversity, community structure, and the health of the reef itself (Lenihan 1999, Plunket 2003, Tolley & Volety 2005, De Santiago et al. 2019). Oyster reefs might therefore act as localized hubs for community organization in estuaries, with trophic structures that differ from (but are connected to) other adjacent habitats (Plunket 2003). The ecosystem functions provided by oysters are at risk globally due to overfishing and habitat degradation, and the Gulf of Mexico is one of the few places left in the

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world where large, viable, consolidated oyster reefs persist (Beck et al. 2011).

Below the community scale, spatial resource partitioning at the inter-species level might be a key driver of faunal heterogeneity among estuarine habitats. For instance, Walton et al. (2022) observed distinct but overlapping distributions of gafftopsail catfish *Bagre marinus* and hardhead catfish *Ariopsis felis* in Apalachicola Bay, Florida, USA. These species have similar life history strategies and trophic function, and they are known to mitigate competition to some extent via habitat partitioning in estuaries of the southern Gulf of Mexico (Yáñez-Arancibia & Lara-Domínguez 1988). In Texas, Cates et al. (2024) speculated that record catches of gafftopsail catfish following an extreme winter storm in 2021 could have been driven by high natural mortality in hardhead catfish, which was one of the most common finfish observed in freeze-kill assessments following the storm (Texas Parks and Wildlife Department 2021). However, mortality-driven tradeoffs could also be influenced by differences in spatial habitat use and subsequent freeze vulnerability, although it is unknown if marine catfish in the northwestern Gulf of Mexico generally (and in Texas specifically) follow similar spatial use patterns to those observed elsewhere in the range of these species. Current adult targeted fishery-independent sampling in Texas uses primarily shoreline-associated gears, and it is unclear whether species associations with more open-water habitats (such as mid-bay subtidal or intertidal oyster reefs) could confound assessments of between-species relative abundance.

At the intra-species level, ontogenetic or demographic variability in preferred habitat characteristics may play a role in linkage of trophic structures associated with those habitats. For instance, ontogenetic shifts among stage-specific habitats in estuaries of the Gulf of Mexico have recently been demonstrated for Atlantic tarpon *Megalops atlanticus* (Kurth et al. 2019), cownose rays *Rhinoptera bonasus* (Ajemian & Powers 2016), and gulf sturgeon *Acipenser oxyrinchus desotoi* (Brogdon et al. 2024), among others. Sex-biased habitat use can similarly provide trophic linkage among distinct habitat types and has been demonstrated in a number of species or assemblages (e.g. stone crab *Menippe* sp.: Wilber 1989; red drum *Sciaenops ocellatus*: Gold & Turner 2002; blue crab *Callinectes sapidus*: Harding & Mann 2010; and coastal sharks: Drymon et al. 2020). Detection of ontogenetic or sex-biased habitat selection would necessarily be the first step in identifying significant links among trophic structures that manifest at the demographic scale.

Oyster reefs are a substantial habitat feature dispersed throughout the estuaries of Texas and occur along shorelines or in the open bay. However, mid-bay oyster reefs are not included in long-standing fishery-independent monitoring practices in Texas, as the gears meant to target adult, large-bodied organisms in these assessments are primarily deployed along shorelines. In this study, we took advantage of a long-running fishery-independent sampling effort in East Matagorda Bay, Texas, to examine the biotic diversity residing along mid-bay reef areas at the community level, species level, and demographic level, and to contrast that diversity against the biota observed adjacent to undifferentiated shoreline habitats. We use the term 'undifferentiated shoreline habitats' here (and throughout this text) as a catch-all term that refers to the varied shoreline types found throughout East Matagorda Bay. These include seagrass meadows, stands of marsh vegetation, intertidal oyster reefs, and undifferentiated mud bottom areas, all of which are currently sampled through routine monitoring practices. We tested the null hypothesis of system-wide homogeneity at multiple scales, asking 3 overlapping experimental questions: (1) Are there detectable, significant differences in community structure on mid-bay oyster reef habitats versus undifferentiated shoreline habitats? (2) Are there detectable differences at the species level in catch rates or mean size between mid-bay oyster reefs and shorelines? (3) Are there detectable differences in the demographics of spotted seatrout *Cynoscion nebulosus* that are associated with mid-bay oyster reefs versus shorelines? The spotted seatrout is a mid-trophic predatory species and is one of the most popular game fish in the greater Gulf of Mexico, and also one of the most intensively managed (Nelson et al. 2021). This species was chosen as a case study for its importance as a recreational fishery target, as well as its outsized impact on estuarine trophic structures as a common mesopredator. Overall interpretations from these data can be used to improve the decision-making process for fisheries and habitat management at multiple scales and add clarity to the spatial units required to observe the community, species, and demographic-level heterogeneity that can be expected in estuarine systems.

2. MATERIALS AND METHODS

2.1. Study area and sampling strategy

East Matagorda Bay (EMB) is an approximately 14800 ha estuary bounded by the Colorado River

watershed on the west, Caney Creek on the east, and Matagorda Peninsula on the south (Fig. 1). Although adjacent to the lower Colorado River basin, the estuary receives minimal freshwater inflow from the Colorado River due to diversion of the primary channel into West Matagorda Bay (diversion channel was completed in 1991). Other freshwater sources include Caney Creek to the east and Peyton Creek/Lake Austin to the north. A single permanent access point to the Gulf of Mexico (Mitchell's Cut) exists on the eastern end of EMB, although ephemeral flow to and from the Gulf might also occur at other access points along the peninsula during exceptionally high tide or flood events. Water parameters in EMB vary seasonally and spatially, but the estuary has a mean annual salinity of 25 psu and a mean bottom temperature of 23°C, and is relatively shallow with a mean depth of 1.6 m (maximum 4.5 m). The system is characterized primarily by

mud bottom, with numerous mid-bay oyster reefs that have complex relief patterns, including some that are exposed during mean low tide (intertidal reefs).

As part of its fishery-independent routine monitoring program, the Texas Parks and Wildlife Department (TPWD) uses experimental gill nets to sample the adult finfish population for 10 wk in spring (April–June) and fall (September–November) each year in estuaries throughout the Texas coast, including EMB. Experimental nets are normally set adjacent and perpendicular to shorelines to simultaneously minimize conflicts with boating activity and sample a broad range of depths from the shoreline into open water. These routine deployments sample the entire range of shoreline-associated habitats encountered in EMB.

We took advantage of routine gill net sets in EMB by pairing scheduled shoreline deployments with additional open water, mid-bay reef-associated de-

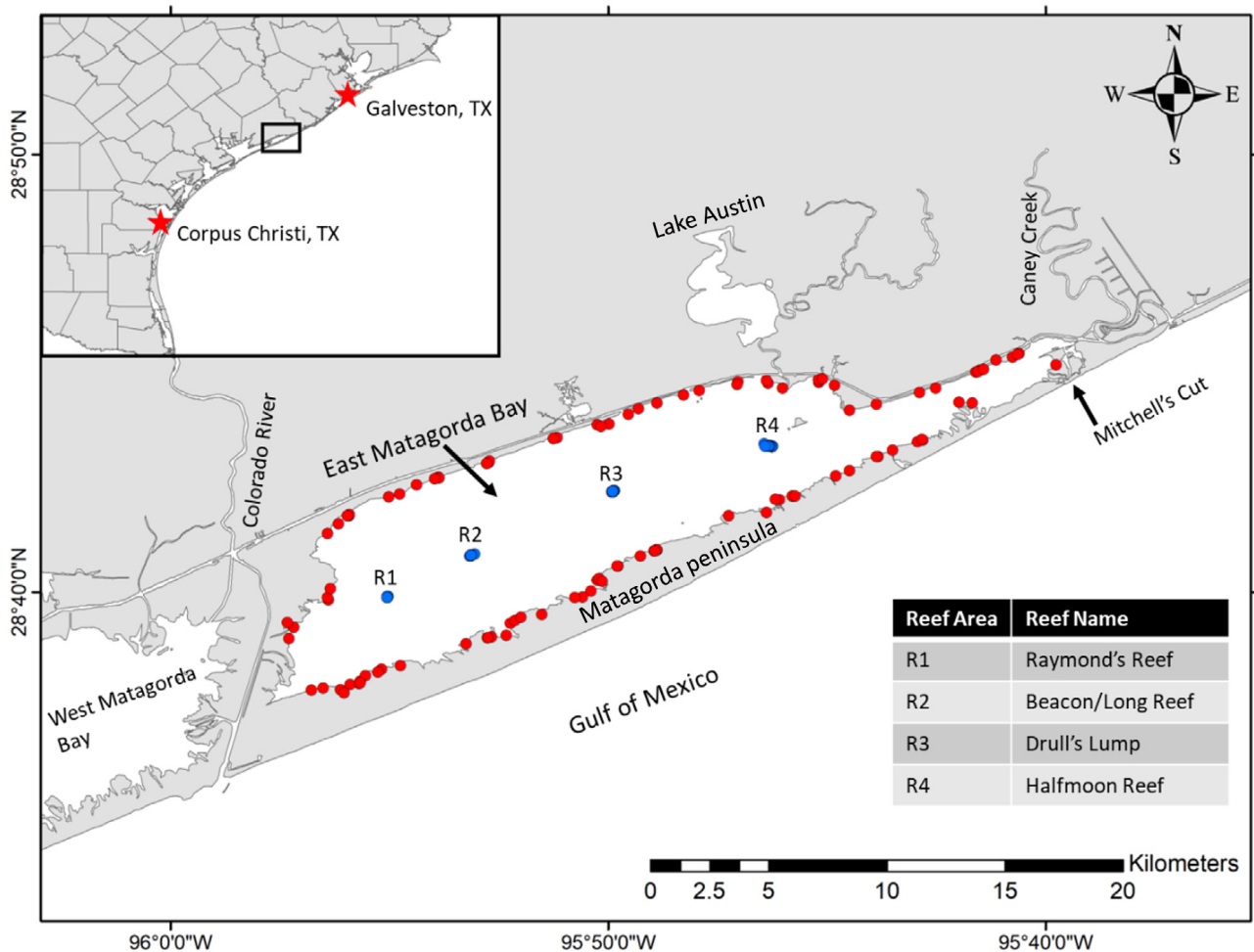


Fig. 1. East Matagorda Bay, Texas (USA), and surrounding area, including gill net sampling locations along shorelines ($n = 104$, red dots) and mid-bay reef areas ($n = 59$, blue dots). Multiple samples at each reef area are stacked so true reef sample sizes are not well represented here. In any given week, reef sample locations were chosen so that they were paired spatially with 1 of 2 scheduled, routine monitoring gill net sets. The extent of the study area relative to the coastline of Texas is indicated in the inset

poyments for 3 yr (2005–2007). These extra nets were set adjacent to known mid-bay consolidated oyster reefs during the same 10 wk time periods during which shoreline deployments took place. Reef areas were chosen that had a crown at or above the surface at mean low tide, and in areas that were not immediately adjacent to the shore (>1000 m from the nearest shoreline). Four intertidal reef areas that had these characteristics were ultimately used for mid-bay sampling; reef areas varied in size from 32 425 to 147 010 m² in total area. All 4 areas had living reef formed primarily by eastern oysters *Crassostrea virginica* as the main bottom type, with interspersed shell hash and mud bottom. The reefs were distributed along the long axis of the bay (aligned generally from west to east), which allowed reef samples to be paired with semi-adjacent shoreline samples on the same day. Overall, this sampling strategy resulted in uneven sample sizes between shorelines and reefs (2 routine shoreline sets, 1 reef set per week; Table 1), as well as an imperfect spatial sampling design (Fig. 1), but it was nevertheless necessary for 2 reasons: (1) a desire to take advantage of existing fishery-independent monitoring shoreline samples as 'control' samples, the locations of which were chosen based on a predetermined, stratified random sampling grid design, and (2) there were a limited number of reef areas that fit the criteria for experimental gill net sets.

All gill nets were mono-filament nets with four 45.7 m long by 1.2 m deep panels, with mesh sizes in each panel that became progressively larger from either shoreline or reef crown to open water (76, 102, 127, and 152 mm). Each net was set in the top of the water column and deployed within 1 h of sunset and retrieved within 4 h of sunrise on the next day. Water quality parameters (temperature [°C], salinity [psu], dissolved oxygen [mg l⁻¹]) were measured at the time of deployment using a YSI Professional water quality meter. Depth was measured to the nearest 0.1 m at the deep end of the net using a marked PVC pole. Turbidity was determined by taking a water sample at the time of deployment and measuring the sample to the

nearest nephelometric turbidity unit (ntu) using a Hach turbidimeter upon return to the lab. The first 19 individuals of each species, in each mesh, were measured to the nearest mm total length (TL) upon net retrieval and then released. The remainder of individuals were counted but not measured, with the exception of spotted seatrout in the first 2 yr of the study, all of which were retained for age and maturity analysis (Section 2.4). The distribution of total catch (total number of organisms caught per net) was compared between reef- and shoreline-associated nets, in spring versus fall, using generalized least squares and ANOVA.

2.2. Community structure analysis

Detrended correspondence analysis (DCA; Hill & Gauch 1980, Oksanen & Minchin 1997) was used as an initial exploratory technique to observe multi-species patterns of catch among gill net samples. For this analysis, catch of each species in each net (n net⁻¹) was transformed by applying a Hellinger transformation (Legendre & Gallagher 2001) to the raw catch data to convert absolute species abundance to relative abundance. The analysis was further limited to species that accounted for ≥0.1% of the total catch to eliminate the impact of transient/rare taxa. One assumption of this analysis was that catch in each net occurred over roughly the same level of effort given the systematic overnight soak times study-wide, although we acknowledge that effort was not the same across all net deployments due to moderate seasonal changes in day length that impacted on soak time. Each gill net sample was plotted based on loading scores along the first 2 DCA axes of ordination to qualitatively assess whether there were differences in ordination space between area types (mid-bay reef versus undifferentiated shoreline). Loadings of original variables (species) along each ordinated axis were used to determine whether there were suites of species driving ordination patterns among samples. Preliminary DCA (and other community analyses) were parsed by season, but after observing that habitat area drove most of the variation in the DCA bi-plot, we combined seasons for community assessments.

Upon observation that reef and shoreline samples were best distinguished along the first axis of ordination (DCA1, see Section 3.2), we used stepwise regression of measured water parameters (temperature, salinity, dissolved oxygen, turbidity, and depth) to build a statistical model to predict loading of each gill net sample on DCA1. Water parameter variables were

Table 1. Seasonal gill net sample size adjacent to reefs and along shorelines in East Matagorda Bay for the 3 years included in this study

Year	Fall		Spring	
	Reef	Shoreline	Reef	Shoreline
2005	9	16	10	17
2006	10	17	10	18
2007	10	17	10	19

modeled as continuous and were all included in the initial regression model. Variables with the lowest explanatory power (based on model sum of squares) were then removed from the model sequentially until all were removed. We chose the model that minimized the Bayesian information criterion (BIC) using this stepwise approach as the final model for predicting DCA1. ANOVA was used to test for univariate differences in mean values of each of the abiotic variables that were included in the final model.

SIMPER (Clarke 1993) was used to assess which species were primarily responsible for the differences among the reef and shoreline communities. For comparative purposes, we also performed an indicator species analysis, which identifies taxa that are indicative of a particular group (Dufrene & Legendre 1997). Fidelity to a group is computed as the number of samples in a group (groups = reef versus shoreline) where a particular species is present divided by the total number of samples in the group. Indicator values are percentages that range from 0 to 100. Statistical significance of the indicator values was estimated by 10 000 random reassignments of samples across groups (reef versus shoreline), and a simple Bonferroni correction was applied to adjust for multiple simultaneous tests.

Raw catch data were used to determine the per-sample species richness (number of species) and species diversity based on the Shannon diversity index. We then computed the average species richness and diversity for reef and shoreline over all gill net deployments. A 1-way ANOSIM (Clarke 1993) was used to determine whether there was a significant difference in the species composition of reef and shoreline communities based on the Bray & Curtis (1957) distance. Species richness and diversity estimates, ANOSIM, SIMPER, DCA, and indicator species analysis were carried out using the computer freeware PAST, version 4.13 (Hammer et al. 2001). Hellinger transformation was performed using the 'vegan' (Dixon 2003) package in R (R Core Team 2023).

2.3. Species-specific comparisons of catch and size

Differences in catch ($n \text{ net}^{-1}$) and length (TL for fish and carapace width for crabs; mm) were assessed between area (shoreline versus reef) and season (spring versus fall) using generalized least squares (GLS) procedures for the 5 most abundant finfish, 2 most abundant invertebrates, and all shark species combined captured in gill net surveys during the study period (Table 2). The most abundant finfish

captured during the study period consisted of 3 species of Sciaenidae (red drum, spotted seatrout, black drum *Pogonias cromis*) and 2 Ariidae species (hardhead catfish, gafftopsail catfish). The 2 most abundant invertebrate species captured during this period were blue crabs and gulf stone crabs *Menippe adina*. These were the only 2 invertebrate species commonly captured in the gill net surveys. Sharks captured during the study period included the following species: blacktip shark *Carcharhinus limbatus*, Atlantic sharpnose shark *Rhizoprionodon terraenovae*, spinner shark *C. brevipinna*, scalloped hammerhead *Sphyrna lewini*, bonnethead *S. tibero*, finetooth shark *C. isodon*, dusky shark *C. obscurus*, and bull shark *C. leucas*. All shark species were combined for analysis due to limited sample size for any single species but a desire to evaluate these species as an aggregate top predator group. Analysis on shark length was not conducted due to expected differences in asymptotic length among species. Weighted least-squares procedures were applied in the GLS framework when heterogeneity of variance was observed in plotted residuals between factor levels of the predictor variables (i.e. location and season). This allowed for constant variance structures within levels of these variables (Zuur et al. 2009). Final models were selected by minimizing Akaike's information criterion (Akaike 1973). When variable interaction (i.e. area \times season) was detected, Tukey-style multiple comparisons with a Westfall adjustment of p-values were conducted to assess differences in catch or length between shoreline and reef areas within each level of season. When variable interaction was not detected, the interaction variable was dropped so that area and season were assessed as additive variables. Statistical relationships were deemed significant at $\alpha = 0.05$. All GLS analyses were conducted in R using the 'nlme' package (Pinheiro et al. 2023) and the 'multcomp' package (Hothorn et al. 2008).

2.4. Comparisons of size, age, and maturity of spotted seatrout

Spotted seatrout were retained from all nets in 2005 and 2006 and transported on ice to the Perry R. Bass Marine Fisheries Research Station for analysis of size, age, and sexual maturity. Individual TL was measured to the nearest mm; if TL was not available due to deterioration of the tail (a common occurrence for entangled spotted seatrout that have been depredated by crabs or other organisms), standard length (SL) was measured to the nearest mm and then converted to TL by using the equation:

Table 2. Total captured, occurrence in gill net samples (n = 163 nets) (% occurrence in gill net samples) of finfish and invertebrates captured in gill net surveys during the study period. Mean length (SE) was the average of total length for all individuals in the study

Species	Total captured	Occurrence	Mean length (mm)
Red drum <i>Sciaenops ocellatus</i>	2933	161 (98.8)	498 (2)
Hardhead catfish <i>Ariopsis felis</i>	2478	155 (95.1)	338 (1)
Spotted seatrout <i>Cynoscion nebulosus</i>	2365	160 (98.2)	465 (2)
Black drum <i>Pogonias cromis</i>	2250	139 (85.3)	427 (2)
Gafftopsail catfish <i>Bagre marinus</i>	1479	130 (79.8)	517 (2)
Gizzard shad <i>Dorosoma cepedianum</i>	860	111 (68.1)	355 (1)
Atlantic croaker <i>Micropogonias undulatus</i>	706	127 (77.9)	291 (1)
Spot <i>Leiostomus xanthurus</i>	661	99 (60.7)	248 (1)
Sheepshead <i>Archosargus probatocephalus</i>	303	96 (58.9)	406 (4)
Blue crab <i>Callinectes sapidus</i>	294	74 (45.4)	157 (1)
Gulf menhaden <i>Brevoortia patronus</i>	277	55 (33.7)	245 (2)
Striped mullet <i>Mugil cephalus</i>	215	72 (44.2)	382 (3)
Sand seatrout <i>Cynoscion arenarius</i>	106	41 (25.2)	348 (4)
Southern flounder <i>Paralichthys lethostigma</i>	98	55 (33.7)	406 (6)
Gulf stone crab <i>Menippe adina</i>	49	38 (23.3)	99 (3)
Alligator gar <i>Atractosteus spatula</i>	48	23 (14.1)	1075 (30)
Blacktip shark <i>Carcharhinus limbatus</i>	46	17 (10.4)	682 (23)
Atlantic spadefish <i>Chaetodipterus faber</i>	45	23 (14.1)	181 (7)
Finescale menhaden <i>Brevoortia gunteri</i>	44	20 (12.3)	294 (6)
Sharpnose shark <i>Rhizoprionodon terraenovae</i>	36	10 (6.1)	595 (16)
Spinner shark <i>Carcharhinus brevipinna</i>	28	11 (6.7)	631 (26)
Scalloped hammerhead <i>Sphyrna lewini</i>	25	14 (8.6)	716 (21)
Pinfish <i>Langodon rhomboides</i>	24	11 (6.7)	221 (9)
Southern kingfish <i>Menticirrhus americanus</i>	23	21 (12.9)	300 (6)
Atlantic stingray <i>Dasyatis sabina</i>	22	16 (9.8)	234 (7)
Bonnethead <i>Sphyrna tibero</i>	15	9 (5.5)	563 (20)
Ladyfish <i>Elops sarus</i>	15	12 (7.4)	464 (23)
Spanish mackerel <i>Scomberomorus maculatus</i>	13	8 (4.9)	444 (14)
Cownose ray <i>Rhinoptera bonasus</i>	10	6 (3.7)	547 (15)
Atlantic tripletail <i>Lobotes surinamensis</i>	10	10 (6.1)	408 (35)
Finetooth shark <i>Carcharhinus isodon</i>	9	6 (3.7)	704 (27)
Gray snapper <i>Lutjanus griseus</i>	9	9 (5.5)	286 (17)
Silver Seatrout <i>Cynoscion nothus</i>	6	3 (1.8)	380 (17)
Pigfish <i>Orthopristis chrysoptera</i>	6	5 (3.1)	228 (7)
Dusky shark <i>Carcharhinus obscurus</i>	5	2 (1.2)	792 (26)
Harvestfish <i>Peprilus paru</i>	4	4 (2.5)	224 (8)
Bull shark <i>Carcharhinus leucas</i>	3	3 (1.8)	987 (2)
Silver perch <i>Bairdiella chrysoura</i>	3	3 (1.8)	212 (30)
Florida pompano <i>Trachinotus carolinus</i>	1	1 (0.6)	351
Spotted gar <i>Lepisosteus oculatus</i>	1	1 (0.6)	204

$$TL = 9.400 + 1.144 \times SL \quad (1)$$

which was based on previous unpublished observations (B. Bumguardner unpubl. data).

Whole individuals were weighed to the nearest 0.5 g using an OHAUS® Champ II Balance digital scale. Gonads were removed and gonad tissues of all females were retained for further reproductive maturity analysis (excluding females with visually decomposing or damaged gonads). An approximately 1 cm² sample of gonad tissue from each female was excised and treated with a clearing solution (6 parts ethanol,

3 parts formalin, 1 part acetic acid; following Brown-Peterson et al. 1988) prior to microscopic evaluation of egg stage. Approximately 15 ml of clearing solution were added to the mass in a 1 oz (~30 ml) vial, capped, and shaken vigorously for approximately 30 s. A subsample of the mixture (approximately 5 ml) was then removed from the vial with a pipette and placed in a petri dish to be examined under a dissecting microscope. A modified version of the criteria of Brown-Peterson et al. (1988) was used for determining the most advanced egg stage observed for each female (1 = primary oocytes/immature, 2 = cortical alveoli

present/early developing, 3 = transitional secondary cortical alveoli/developing, 4 = vitellogenic/first mature, 5 = hydrated/ripe, and 6 = resorbing/spent evidenced by post-ovulatory follicles).

Age was determined by excision and examination of sagittal otoliths. Both sagittal otoliths were removed via dissection, cleaned, and stored dry in paper envelopes. The left sagittal otolith was used for age estimation, but if the left otolith was missing or broken, the right otolith was used. Otoliths were embedded in clear epoxy resin, and sequential 0.3 mm sections were made with a Buehler high-speed Isomet saw until the otolith core was sectioned. The section containing the core was mounted on a glass slide and examined under a dissecting microscope. Linear distances from the otolith core to each annulus and to the otolith margin were obtained using image analysis software and a top-mounted microscope camera, with measurements made along the ventral edge of the sulcus acusticus. Ages were assigned based on a published methodology taking into account the number of annuli present, the date of capture, and an adjustment based on the relative length of the marginal increment (the distance from the outermost annulus to the otolith edge; VanderKooy et al. 2020). All fish were assumed to have hatched on 1 April based on marginal increment analysis from other studies suggesting first deposition in spring (Anderson et al. 2022 and references therein).

To test for differences in spotted seatrout life history characteristics among sample areas, samples were aggregated by location (shoreline versus each reef location, R1–R4; Fig. 1), and ANOVA was used to evaluate the null hypothesis that mean age, TL, or weight did not vary among locations. In the event of a significant ANOVA result, Welch *t*-tests (assuming unequal variances and adjusted for multiple tests performed simultaneously) were used to examine differences in means of each value among areas. Preliminary examination of histograms suggested some left skew in the full distribution of all 3 variables, but the skew was minimal, and it was expected that the ANOVA and associated *t*-tests were robust to this minor violation of assumptions. Upon observation of significantly larger and older males along shorelines as compared to reef areas (see Section 3.4), we combined samples from all 4 reef areas and used comparisons of means and *t*-tests to assess the overall magnitude of observed differences between areas, overall, and then with data parsed by season.

Season-specific length-frequency plots were used to visualize observed differences in spotted seatrout residency across the entire distribution of length for

each sex. After initially noting that the majority of smaller males resided near reefs, and larger males near shorelines, we used logistic regression to estimate the TL at which transition from one habitat to the other occurred in males (based on the supposition that 50% habitat transition occurs at the inflection point of the logistic curve).

Preliminary analysis suggested that most females with mature egg stages (stages 4+) were observed in spring, which is supported by previous research in Texas and the greater Gulf of Mexico that suggest spawning primarily occurs in spring and summer (Brown-Peterson et al. 1988, 2002). We classified spring-caught females as having either immature (stages 1–3) or mature (stages 4+) eggs and used a 2-tailed Fisher's exact test to assess whether there were significant differences in each category between the 2 generalized habitat types. The exact test was executed in JMP software version 17 (SAS Institute).

3. RESULTS

3.1. General catch characteristics

Of the 163 gill net deployments assessed in this study, 59 were associated with mid-bay reefs, and 104 were associated with shorelines (Fig. 1). In most cases, 1 reef-associated net was set simultaneously with 2 semi-adjacent shoreline nets. After removal of outliers and low-frequency species from the data set (for instance, accidental catch of species that are too small to be reliably targeted with large mesh sizes), these 163 gill nets caught 42 species (40 finfish and 2 crab species) and 15 203 total organisms combined. All species captured during the course of the study were native to EMB. The most commonly encountered organism was red drum (observed 2939 times), followed by spotted seatrout (2384 times), hardhead catfish (2190 times), black drum (2163 times), and gaff-topsail catfish (1482 times). Overall, reef and shoreline habitats yielded observations of 35 and 36 species, respectively, with considerable overlap in suites of species. Total catch (count of all organisms encountered in a single net) was normally distributed with a mean of 93 individuals, a minimum of 7 individuals, and a maximum of 221 individuals. Reef-associated nets caught an average of 108 individuals per net, while shoreline-associated nets caught an average of 84 individuals. The model of catch with area and season as predictors indicated that area was a reliable predictor of total catch, but season was not (model $F_{1,161} = 15.7$, $p < 0.001$).

3.2. Community structure analysis

The DCA separated shoreline and reef-associated gill nets along both axes of ordination, but in particular along DCA1 (Fig. 2). On the negative end of DCA1, black drum, gulf menhaden *Brevoortia patronus*, finescale menhaden *B. gunteri*, and sand seatrout *Cynoscion arenarius* were heavily associated with reef samples. Alligator gar *Atractosteus spatula*, southern flounder *Paralichthys lethostigma*, both crab species, striped mullet *Mugil cephalus*, hardhead catfish, and red drum were associated with positive values of DCA1 (mainly representing shorelines). Of the water parameters measured, the best model predicting DCA1 score included only the oxygen and depth variables, although depth was by far the most important predictor, explaining 66% of the overall variance in DCA1 (Table 3). Reef areas were considerably deeper (mean 1.65 m depth) than shoreline areas (mean 0.99 m) but had very similar dissolved oxygen (6.8 mg l⁻¹ on reefs versus 7.2 mg l⁻¹ along shorelines). The ANOVA of depth in each area was significant ($F_{1,161} = 311.1, p < 0.001$), while the ANOVA of oxygen was not ($F_{1,161} = 2.4, p = 0.123$).

The results from SIMPER largely mirrored loading scores from the DCA and indicated that 10 species accounted for 93% of the difference between reef and shoreline communities (Table 4). Of these 10 species, black drum, spotted seatrout, gafftopsail catfish, spot *Leiostomus xanthurus*, Atlantic croaker, and gulf menhaden were more abundant on reefs, whereas hardhead catfish, red drum, gizzard shad *Dorosoma cepedianum*, and blue crab were more common in shoreline habitats. The indicator species analysis also largely confirmed these results. Indicator species for reef habitat included Atlantic croaker, black drum, gafftopsail catfish, gulf menhaden, spot, finescale menhaden, sand seatrout, and scalloped hammerhead. In contrast, alligator gar, gulf stone and blue crabs, hardhead catfish, red drum, southern flounder, and striped mullet were indicative of shoreline habitats.

Mean (\pm SE) species richness differed slightly but significantly between reef (11.78 \pm 0.34) and shoreline (10.54 \pm 0.29), but mean species diversity based on the Shannon diversity index was similar (reef = 1.44 \pm 0.09, shoreline = 1.42 \pm 0.06). The ANOSIM results also indicated that the assemblage

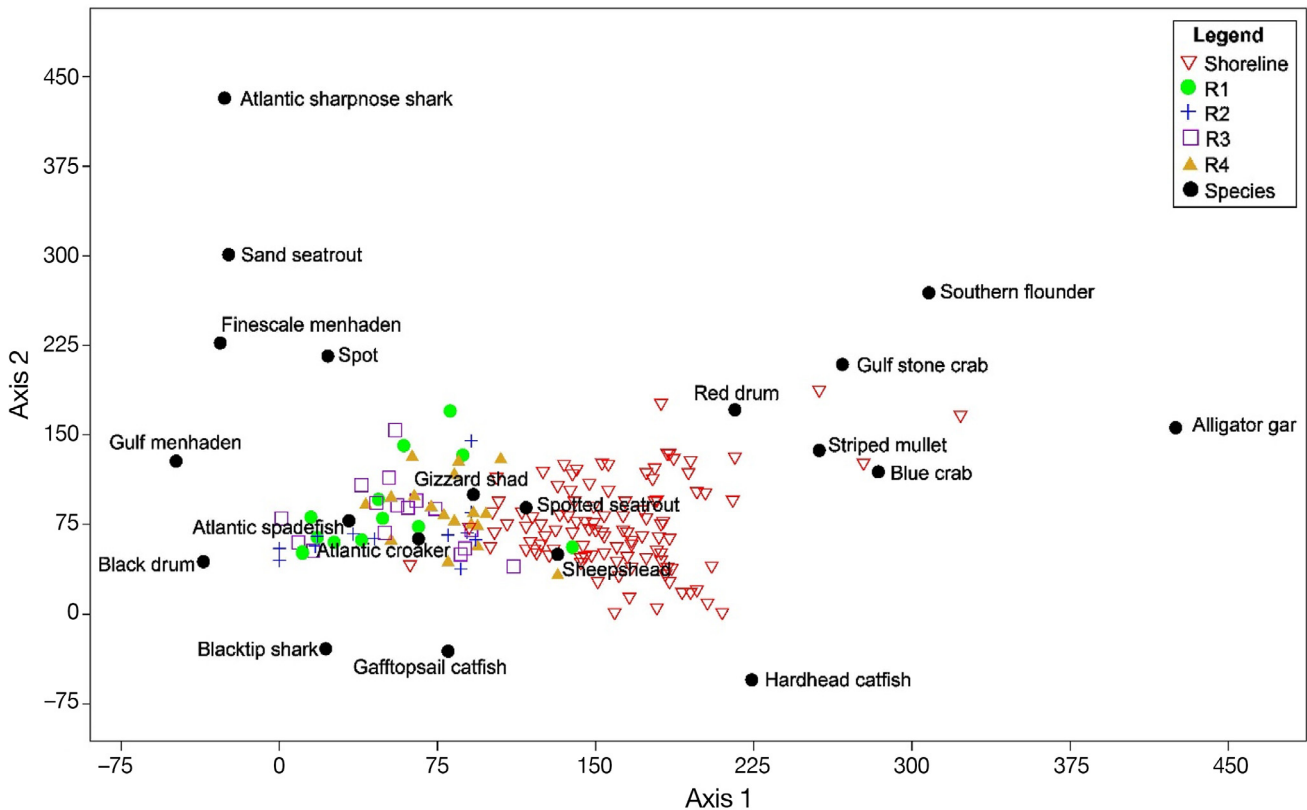


Fig. 2. Detrended correspondence analysis (DCA) scatterplot based on fish assemblages (number of species in reef and shoreline habitats) in East Matagorda Bay. Black dots and labels are species associations with each ordination axis. The position of the species relative to the sites is indicative of their habitat preference

Table 3. Backwards stepwise regression of sample loading scores against principal component axis 1 (PC1), which largely separated shoreline and reef-associated samples. Salinity (Sal), temperature (Temp), turbidity (Turb), dissolved oxygen (Oxy), and depth (Dep) were all initially entered into the regression model, and variables were removed that had the lowest impact on sum-of-squares. Model selection (shaded, step 4 was selected) was made based on minimization of the Bayesian information criterion (BIC)

Step	Parameters	Action	Sequential SS	r ²	BIC
1	Sal, Temp, Turb, Oxy, Dep	All entered	.	0.69	1636
2	Temp, Turb, Oxy, Dep	Sal removed	1120	0.69	1632
3	Turb, Oxy, Dep	Temp removed	2783	0.68	1630
4	Oxy, Dep	Turb removed	1929	0.68	1626
5	Dep	Oxy removed	13490	0.66	1633
6	None	All removed	373005	0.00	1802

Table 4. SIMPER results for East Matagorda Bay pairwise comparisons of reef and shoreline gill nets. For species that contributed >1% to habitat dissimilarity, the habitat type that was most commonly associated is shaded

Species	Average dissimilarity	Contrib. (%)	Mean reef (ind.)	Mean shoreline (ind.)
Black drum	19.17	25.88	42.10	7.13
Hardhead catfish	15.78	21.30	4.67	34.10
Red drum	11.60	15.66	7.21	27.40
Spotted seatrout	5.27	7.12	11.30	9.50
Gafftopsail catfish	4.52	6.11	9.12	4.17
Spot	3.89	5.25	7.48	2.16
Gizzard shad	3.13	4.23	3.32	5.03
Atlantic croaker	3.13	4.22	6.23	2.49
Gulf menhaden	1.55	2.09	2.91	0.43
Blue crab	0.92	1.24	0.13	1.83
Sheepshead	0.73	0.98	1.02	1.02
Striped mullet	0.68	0.92	0.30	1.27
Sand seatrout	0.61	0.82	1.14	0.15
Alligator gar	0.53	0.71	0.00	1.06
Southern flounder	0.50	0.67	0.20	0.89
Atlantic sharpnose shark	0.32	0.44	0.60	0.06
Finescale menhaden	0.22	0.30	0.43	0.03
Atlantic spadefish	0.21	0.29	0.35	0.10
Blacktip shark	0.20	0.28	0.32	0.11
Scalloped hammerhead	0.18	0.25	0.33	0.05
Gulf stone crab	0.17	0.23	0.01	0.33
Spinner shark	0.13	0.18	0.22	0.05
Southern kingfish	0.10	0.14	0.16	0.06
Spanish mackerel	0.08	0.11	0.15	0.01
Bonnethead	0.08	0.10	0.13	0.02
Atlantic stingray	0.06	0.09	0.00	0.13
Ladyfish	0.06	0.08	0.04	0.08
Atlantic tripletail	0.04	0.05	0.01	0.07
Pinfish	0.04	0.05	0.00	0.08
Finetooth shark	0.04	0.05	0.07	0.01
Gray snapper	0.03	0.04	0.00	0.05
Cownose ray	0.02	0.03	0.02	0.03
Dusky shark	0.02	0.02	0.00	0.04
Pigfish	0.02	0.02	0.03	0.00
Bull shark	0.01	0.02	0.00	0.03
Silver perch	0.01	0.01	0.00	0.02
Harvestfish	0.01	0.01	0.02	0.00
Spotted gar	<0.01	0.01	0.00	0.01
Silver seatrout	<0.01	<0.01	0.01	<0.01
Florida pompano	<0.01	<0.01	<0.01	<0.01

structure of reef and shoreline habitats was significantly different ($R = 0.51$, $p < 0.001$).

3.3. Species-specific comparisons of catch and size

The 8 individual species or species groups examined showed significant variation in catch between areas, with spotted seatrout, black drum, gafftopsail catfish, and sharks having greater catch on reef locations, and red drum, hardhead catfish, blue crab, and gulf stone crab having greater catch on shoreline locations (Table S1 in the Supplement at www.int-res.com/articles/suppl/m746p049_supp.pdf). The higher catch of sharks on reefs was driven by higher abundance of every species encountered except for bull shark and dusky shark (Table 5). The greatest disparity in catch between shoreline and reef locations was observed for black drum, hardhead catfish, and red drum (Fig. 3). In addition to the significant season \times location interaction indicated above for red drum, significant seasonal variation in catch was also observed for several other species including spotted seatrout, hardhead catfish, and gafftopsail catfish. All of these species exhibited greater catch during the spring, with hardhead catfish and spotted seatrout showing the greatest disparity between spring and fall catch.

Table 5. Total catch (n) of shark species, study-wide, on reefs (59 nets deployed) versus shorelines (104 nets deployed). Despite lower sampling effort, every shark species except for bull shark and dusky shark were more commonly observed near oyster reefs

Species	Reef	Shoreline
Atlantic sharpnose shark	32	4
Blacktip shark	31	15
Bonnethead	10	5
Bull shark	0	3
Dusky shark	1	4
Finetooth shark	7	2
Scalloped hammerhead	21	4
Spinner shark	21	7

Six of the 7 individual species examined showed significant variation in length between areas (only blue crabs did not yield a significant area relationship). Red drum and black drum were longer at reef locations while spotted seatrout (spring season only), hardhead catfish, gafftopsail catfish, and gulf stone crab (spring season only) were longer at shoreline locations (Table S2). The greatest disparity in length between shoreline and reef locations was for gafftopsail catfish and black drum (Fig. 4). In addition to the several significant season × location interactions indicated above, significant seasonal variation in length was also observed for red drum, gafftopsail catfish, and blue crab. These 3 species were larger in the

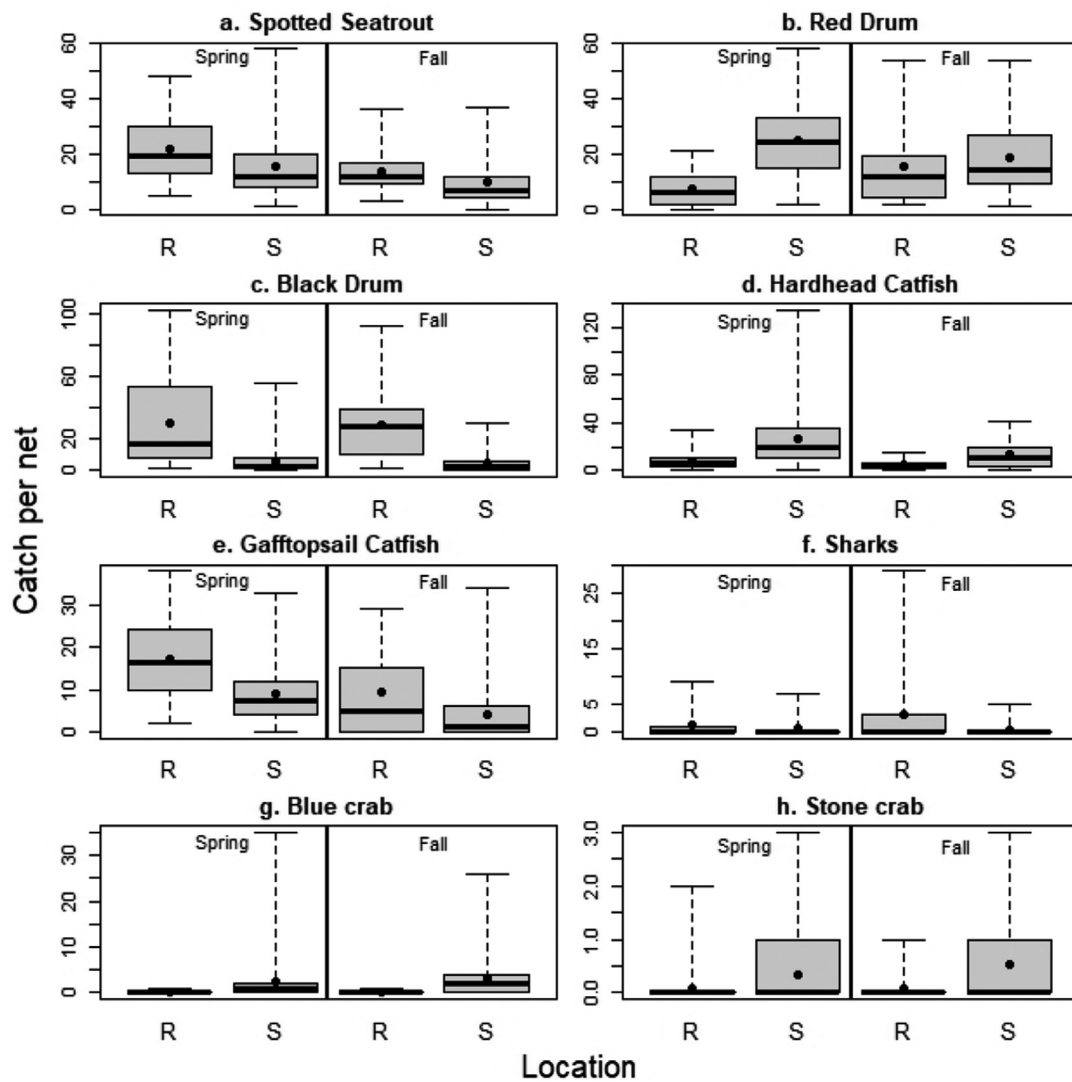


Fig. 3. Catch of selected species in fishery-independent gill net surveys conducted in spring and fall seasons at both reef (R) and shoreline (S) locations. Species include (a) spotted seatrout, (b) red drum, (c) black drum, (d) hardhead catfish, (e) gafftopsail catfish, (f) sharks (all species combined), (g) blue crab, and (h) stone crab. Each box plot includes the following values: mean (solid black dot), median (dark black line), first and third quartile (outside lines of the box), and minimum and maximum values (whiskers)

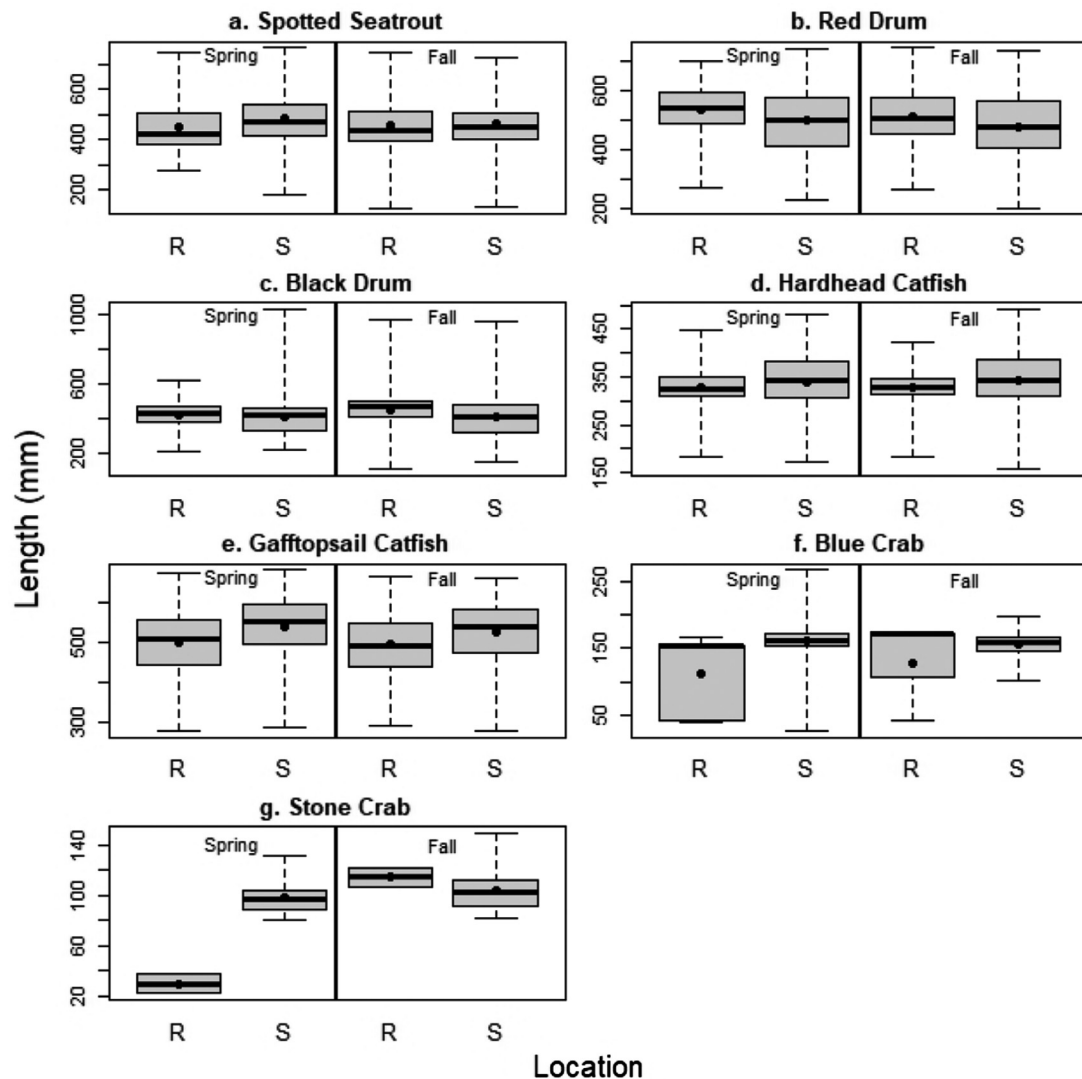


Fig. 4. Length (mm) of specimens for selected species collected in fishery-independent gill net surveys conducted in spring and fall seasons at both reef (R) and shoreline (S) locations. Total length was used for all finfish, and carapace width was used for all crabs. Species include (a) spotted seatrout, (b) red drum, (c) black drum, (d) hardhead catfish, (e) gafftopsail catfish, (f) blue crab, and (g) stone crab. Box plot parameters as in Fig. 3

spring, and the greatest disparity between seasonal lengths was for black drum and red drum (Table S3).

3.4. Comparisons of size, age, and maturity of spotted seatrout

Among female spotted seatrout ($n = 539$ observed), there was a significant difference in overall mean TL observed when comparing disaggregated reef samples (samples broken into individual reefs rather than combined) to undifferentiated shoreline samples ($F_{4,534} = 2.7$, $p = 0.029$). Most reef samples (with the exception of R4, Halfmoon Reef) had smaller ob-

served females than shoreline samples (Fig. 5). Similarly, the ANOVA of males ($n = 425$ observed) also produced similar significant results ($F_{4,420} = 19.79$, $p < 0.001$), with males on all reefs being significantly shorter than those along shorelines.

There was no significant difference in weight among females on reefs versus shorelines in the overall ANOVA ($F_{4,532} = 2.17$, $p = 0.071$). In contrast, the comparison of weight in males was highly significant ($F_{4,419} = 13.45$, $p < 0.001$), with shoreline males being significantly heavier than males on all 4 reef areas.

We found no significant difference in age among females in the overall ANOVA ($F_{4,521} = 1.50$, $p = 0.200$). Males on shorelines were significantly older

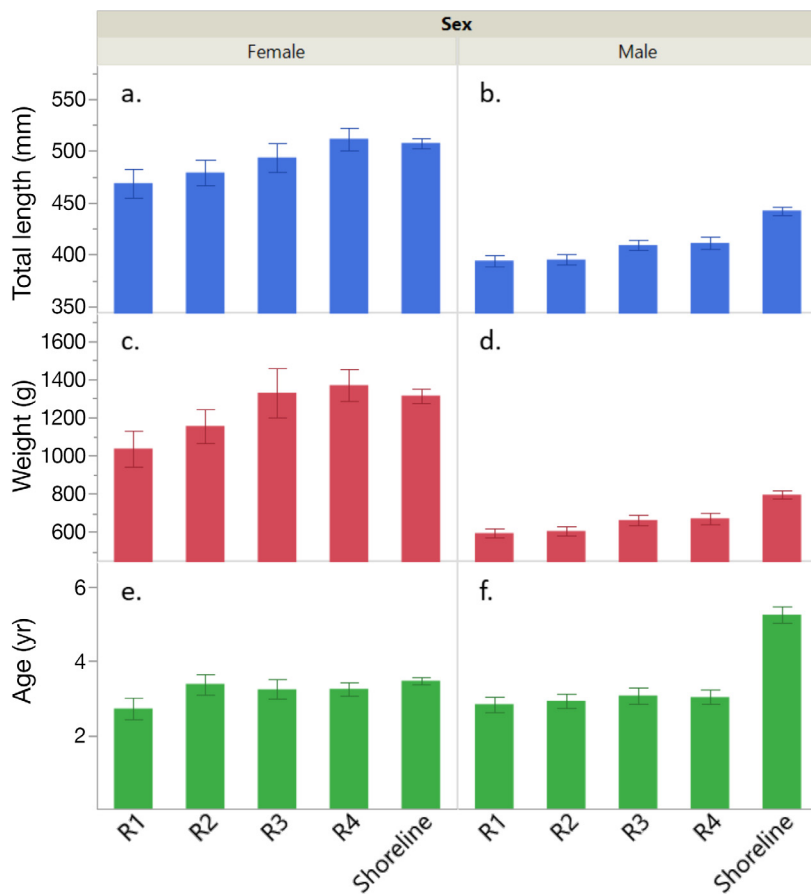


Fig. 5. Differences in total length, weight, and age of spotted seatrout (a,c,e) females and (b,d,f) males in reef (R1–R4) versus shoreline-associated gill net samples. Samples were collected over a 2 yr period (2005–2006) in East Mata-gorda Bay, Texas, using gill nets. Error bars represent standard error in each area type

than those in reef areas ($F_{4,401} = 27.92$, $p < 0.001$), and this finding was significant across all shoreline/reef pairwise comparisons.

Overall, male spotted seatrout observed along shorelines were 39 mm longer, 205 g heavier, and 2.2 yr older than their counterparts observed near reefs, and these differences were more exaggerated in spring than in fall (Table 6). While the distributions of female TL between shorelines and reefs were qualitatively similar, there was a clear difference in size distribution of males along shorelines versus near reefs (Fig. 6). The logistic regression analysis of male TL against location was significant ($z = 7.18$, $df = 431$, $p < 0.001$) and suggested that 50% of males associated with mid-bay reefs move to shoreline habitats at approximately 457 mm TL (between ages 4 and 5 based on size-at-age).

The Fisher exact test meant to test for differences in female egg maturity was not significant ($\chi^2 = 0.736$, $p = 0.443$), suggesting there were no differences in

the distribution of mature egg stages between shoreline and reef females observed in spring collections (Fig. 7). A majority of females (~95%) had eggs that were classified as stage 4 (vitellogenic) in both habitats.

4. DISCUSSION

The community structure associated with mid-bay oyster reefs in EMB was observably different from community structure associated with shorelines, and those differences tended to be driven by (1) depth on the abiotic side and (2) divergent habitat use at nested taxonomic and demographic scales on the biotic side. Admittedly, this study was not well designed to test whether it was the presence of oyster reef specifically rather than differences in abiotic characteristics (e.g. depth) that drove observed community differences between reef and shoreline. However, several previous studies have described the importance of oyster reef as habitat and as a driver of estuarine community structure (e.g. Lenihan 1999, Plunket 2003, Tolley & Volety 2005, Stunz et al. 2010, Beck et al. 2011, De Santiago et al. 2019, La Peyre et al. 2019). In any event, at the species scale, there were

significant differences in catch rates of several prominent, common species between shorelines and mid-bay reefs, many of which are important targets for recreational or commercial fisheries. Red drum, spotted seatrout, black drum, blue crab, and gulf stone crab are all important fishery targets in Texas, either in the commercial or recreational sense (or both), and all appear to show significant deference to one habitat type or the other. Previous studies suggest that spatially explicit stock assessments that account for heterogeneity in habitat use may perform better than assessments that are naïve to spatial heterogeneity (Punt 2003, Callihan et al. 2013, Truesdell et al. 2016), and the spatial complexity of the current data supports those findings. Stock assessments that are based on an imperfect understanding of spatial heterogeneity can lead to biologically inaccurate estimates of key population parameters such as mortality and spawning stock biomass (Guan et al. 2013). More broadly, one of the key interpretations from our study

Table 6. Length, weight, and age (mean \pm SE) of male spotted seatrout captured along shorelines versus adjacent to mid-bay reefs in East Matagorda Bay (a) overall, (b) in spring, and (c) in fall. The statistical test applied in each case was Welch's *t*-test assuming unequal variances. Males along shorelines were longer, heavier, and older than males observed at mid-bay reef areas, and the difference was especially pronounced in spring

	Shoreline	Reef	Difference	<i>t</i>	df	<i>p</i>
(a) Test (overall)						
Total length (mm)	443 (\pm 3.8)	404 (\pm 2.8)	39 (CI 29–48)	8.1	296	<0.0001
Weight (g)	843 (\pm 33.3)	638 (\pm 25.0)	205 (CI 101–309)	3.9	171	<0.0001
Age (yr)	5.2 (\pm 0.17)	3.0 (\pm 0.12)	2.2 (CI 1.8–2.6)	9.2	204	<0.0001
(b) Test (spring males)						
Total length (mm)	462 (\pm 5.3)	402 (\pm 3.3)	60 (CI 48–72)	9.7	264	<0.0001
Weight (g)	915 (\pm 27.4)	645 (\pm 16.7)	270 (CI 207–333)	8.4	263	<0.0001
Age (yr)	6.6 (\pm 0.24)	3.1 (\pm 0.14)	3.5 (CI 2.9–4.0)	12.5	251	<0.0001
(c) Test (fall males)						
Total length (mm)	425 (\pm 5.2)	407 (\pm 5.1)	19 (CI 7–33)	2.6	157	0.0115
Weight (g)	686 (\pm 22.2)	611 (\pm 21.8)	75 (CI 14–137)	2.4	157	0.0164
Age (yr)	4.1 (\pm 0.22)	2.6 (\pm 0.21)	1.5 (CI 0.9–2.1)	4.89	151	<0.0001

is that management actions that are meant to modify the regulatory status of key fishery species might have disproportionate impacts on trophic structures associated with the habitat types preferred by those species.

Coastal shark catches were an example of the spatial heterogeneity inherent in our data. As an aggregate, sharks were 5 times more likely to be observed

along mid-bay reefs than along shorelines in EMB. Only 2 sharks were more commonly observed along shorelines versus reefs, dusky shark and bull shark. Previous studies have suggested that bull sharks (particularly juveniles) are more likely to be encountered in upper estuaries, perhaps as a mechanism for avoidance of larger predatory sharks (Matich et al. 2020, Lofthus et al. 2024). Although EMB does have ephemeral freshwater inputs from small local drainages, there are no major rivers that feed this estuary, which more typically resembles a coastal lagoon than a true estuary with respect to mean water qualities (e.g. relatively high salinity driven by low inflow; Neupane & Schoenbaechler 2023), which may limit this bay with regard to habitat quality for bull sharks. In addition to the unexpectedly low abundance of bull sharks, the overall composition of the shark assemblage in EMB was also qualitatively different than previous observations on the greater Texas coast (e.g. Froeschke et al. 2010, Plumlee et al. 2018), which have primarily been based on shoreline-associated gill net catches by TPWD (Froeschke et al. 2010, Matich et al. 2017, 2020, Plumlee et al. 2018, Lofthus et al. 2024). In contrast, Swift & Portnoy (2021) used open water, demersal long-line catches during what is likely to be the peak annual timing of presence for coastal sharks in

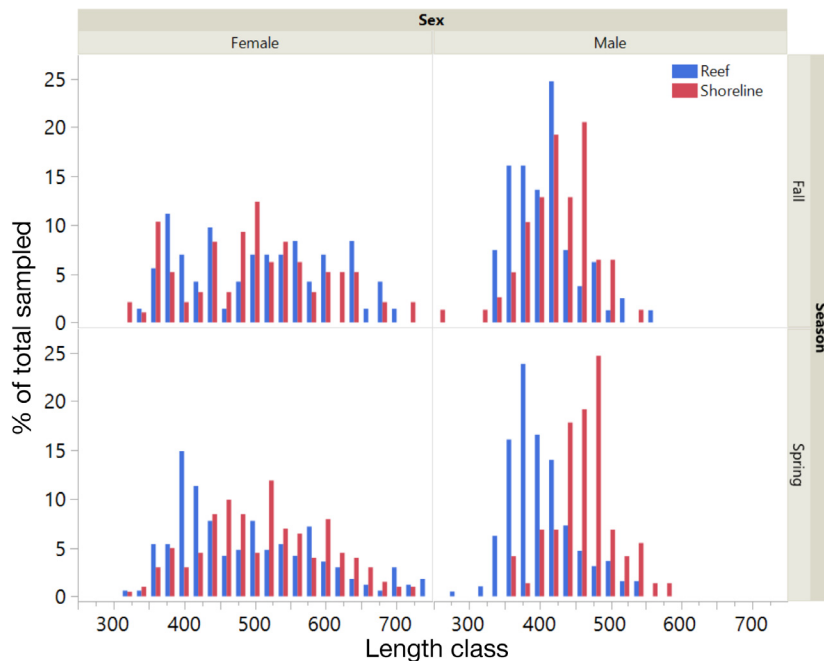


Fig. 6. Length-frequency plots of female and male spotted seatrout capture near reefs (blue) and along shorelines (red). The y-axis is the percentage of raw individual counts that fell into each length bin. Samples were split between spring and fall to observe season-specific spatial use patterns

along mid-bay reefs than along shorelines in EMB. Only 2 sharks were more commonly observed along shorelines versus reefs, dusky shark and bull shark. Previous studies have suggested that bull sharks (particularly juveniles) are more likely to be encountered in upper estuaries, perhaps as a mechanism for avoidance of larger predatory sharks (Matich et al. 2020, Lofthus et al. 2024). Although EMB does have ephemeral freshwater inputs from small local drainages, there are no major rivers that feed this estuary, which more typically resembles a coastal lagoon than a true estuary with respect to mean water qualities (e.g. relatively high salinity driven by low inflow; Neupane & Schoenbaechler 2023), which may limit this bay with regard to habitat quality for bull sharks. In addition to the unexpectedly low abundance of bull sharks, the overall composition of the shark assemblage in EMB was also qualitatively different than previous observations on the greater Texas coast (e.g. Froeschke et al. 2010, Plumlee et al. 2018), which have primarily been based on shoreline-associated gill net catches by TPWD (Froeschke et al. 2010, Matich et al. 2017, 2020, Plumlee et al. 2018, Lofthus et al. 2024). In contrast, Swift & Portnoy (2021) used open water, demersal long-line catches during what is likely to be the peak annual timing of presence for coastal sharks in

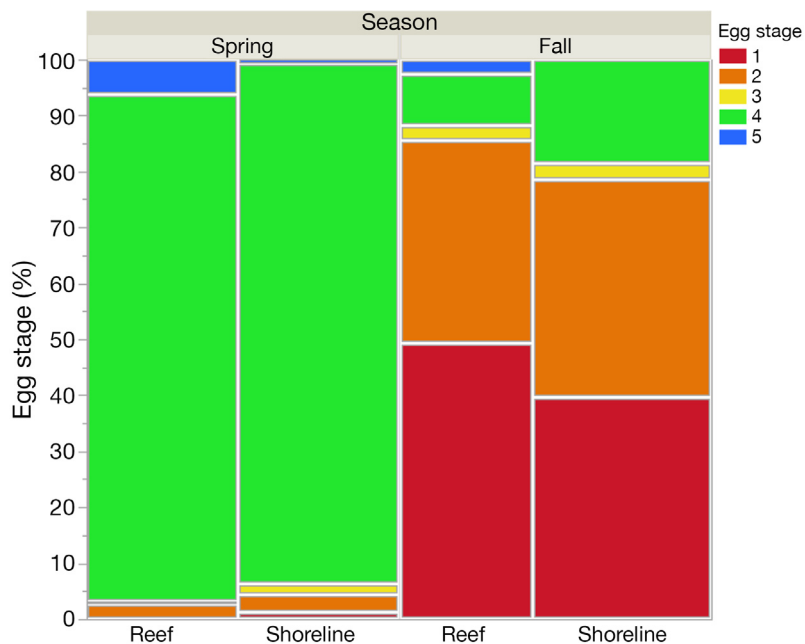


Fig. 7. Relative % of egg stages observed in female spotted seatrout on reefs, versus along shorelines, in spring and fall for 2 years of combined data collection (2005, 2006). When aggregated into immature (stages 1–3) and mature egg stages (stages 4+), there were no differences in egg stages between reef or shoreline females

Texas (July–August) and observed suites of elasmobranchs that were qualitatively more similar to the current data. The relative abundance of the species making up the taxonomic suite of sharks inhabiting Texas estuaries varies seasonally, spatially, and among gear types, and oyster reefs appear to be important habitat holding a variety of shark species that are less common along shorelines (although it is unknown whether this latter finding is representative of other Texas estuaries, or simply a unique feature of EMB).

Another finding in the current data set that was surprising was the pattern of blue crab and gulf stone crab catch rates on shorelines (relatively high catch) versus reefs (relatively low catch). Juvenile crabs are known to use oyster reefs as protective habitat from predators (Macreadie et al. 2012, Longmire et al. 2021). Additionally, eastern oysters have been shown to be an important part of the diet of adult crabs (e.g. Laughlin 1982); for instance, in some cases, blue crab predation on oyster reefs is so intensive as to cause localized extinction of juvenile-stage oysters (Eggleston 1990a,b). Given the importance of oyster reefs at multiple life stages, our expectation was that relative abundance of both crab species would be higher near reefs than along shorelines, but instead, the opposite pattern was observed. This may on one hand imply a capture bias; some evidence exists for behavioral differences of blue crabs in different habitat types

(Laughlin 1982, Byers et al. 2017), and blue crab activity levels on oyster reefs have been shown to be impacted by the presence of predators (Byers et al. 2017) among other factors. The relatively high abundance of predatory shark species (in particular, bonnet-head sharks) might reduce activity of blue crabs on mid-bay reefs, resulting in fewer interactions with the passively fishing gill net gear deployed in the study. On the other hand, the higher relative abundance of crabs along shorelines could have been driven by use of shoreline-associated habitats (e.g. marsh, seagrass, intertidal reef) that were undifferentiated in this study. In Galveston Bay, TX, Zimmerman et al. (1989) found that blue crabs were significantly more abundant in shoreline marsh habitats than on oyster reefs, and this pattern was repeated across 2 sampling seasons (although the same study found the opposite pattern for gulf stone crabs, which were more common on oyster reefs).

In any event, it is likely that salt marsh and oyster reefs, both of which are common in EMB, both provide critical habitat for multiple life stages of crab species in general (Coen et al. 1999), and transient or seasonal use of reef habitats may have been under-represented here due to a variety of factors, ultimately leading to sample bias. It is nevertheless clear that habitat has the potential to impact the assessment of crab populations (either in the form of behavior or discrete habitat preference), and spatial habitat use should thus be considered for future analyses (when data exist) as well as in planning for future management actions.

Below the level of inter-species comparisons, spotted seatrout are an excellent case study of how estuarine habitat use varies at the intra-specific (i.e. demographic) scale. Although spotted seatrout were more commonly observed along reefs, they were frequently observed in both habitat types, and as a result they were not indicators of either area type. However, there were stark demographic differences among the population segments inhabiting reefs versus shorelines. Spotted seatrout along shorelines were generally larger and older than those inhabiting reef areas, and this difference was especially pronounced for males, and even more pronounced in the spring. Generally speaking, populations of fishes existing within estuaries are unlikely to exhibit spatial homo-

geneity, and a failure to understand population dynamics and spatial heterogeneity at the ecological or demographic scale risks localized extinction and creates uncertainty for the population at the estuary scale (Punt 2003, Holland & Herrera 2012). Moreover, highly mobile species (such as spotted seatrout) can drive nutrient flows across ecosystems (Peller et al. 2022), and these flows may ultimately be impacted by the timing of ontogenetic habitat shifts such as from reefs to shorelines in older, larger males. The effects of partial migration (directed movements by a subset of a larger population) can be unintuitive but otherwise have outsized impacts on the drivers of diversity and function in ecosystems (Peller et al. 2023). To our knowledge, age- or size-based transition of a large fraction of the male spotted seatrout population specifically from reef to shoreline has not been previously described. However, Callihan et al. (2013) reported 2 findings that are qualitatively similar to those described here using acoustically tagged male and female spotted seatrout in Calcasieu Lake, LA: (1) males were 2–3 times more likely than females to emigrate permanently from the estuary, and (2) sex-biased migration was most pronounced in the spring. There have now been repeated observations of significant sex-biased spatial distribution patterns of spotted seatrout associated with the spawning season (Lowerre-Barbieri et al. 2009, Callihan et al. 2013, this study). One key takeaway from all of these observations is that even if species appear to use multiple habitat types commonly and therefore do not rise to the level of 'keystone' for either habitat type, ontogenetic or gender-driven differences in habitat use (or both) might result in hidden differences that impact the success of species-specific conservation, and that also impact energy flows between distinct trophic structures.

Despite differences in overall community structure, metrics of species diversity were similar between shoreline-associated and reef-associated samples. Each area type caught approximately the same number of species (35 along shoreline, 36 near reefs, with a great deal of overlap), and per-sample richness and diversity estimates were similar. The contrasting patterns of diverging community structure versus numerical similarity in community diversity metrics may be an indication that each generalized habitat type possesses similar trophic frameworks, but that trophic functions that make up those frameworks might be performed by slightly different actors. Recent studies of species richness and diversity in Texas estuaries have demonstrated increasing diversity coastwide (Fujiwara et al. 2019, Pawluk et al.

2021), possibly driven by climate change and increasing abundance of tropical species that are expanding their range (Pawluk et al. 2021, 2022). However, functional dispersion (variance in species traits within a defined space, in this case an estuary) declined along the same time frame, suggesting homogenization of functional traits across the estuarine space. This same type of functional homogenization might exist between habitats (below the estuary scale) in an equilibrium state; for instance, species that are similar ecologically or that perform overlapping trophic functions might be practicing habitat partitioning to reduce competition. An example of this phenomenon in the present work is the distribution of marine catfish in the family Ariidae; while hardhead catfish were indicator species along shorelines, gafftopsail catfish were indicator species along mid-bay reefs. Both species are generalist consumers with a great deal of niche overlap (Olsen & McCulloch 2024), and Cates et al. (2024) suggested that recent declines in growth of hardhead catfish in Texas could be explained by the increasing abundance of gafftopsail catfish, implying interspecific competition. The differences in abundance of these 2 species on shorelines versus reefs may therefore be a mechanism of limiting interspecific competition through spatial partitioning. Another example of the same phenomenon is the contrasting patterns between alligator gar (shoreline specialist) versus coastal sharks (reef-associated). A recent investigation of these 2 top predator groups in Texas coastal areas similarly suggested niche overlap that was compensated for by spatial partitioning (Marsaly et al. 2023). Ecological implications aside, these findings generally highlight the value of assessing 'diversity' with both univariate metrics (i.e. richness, Shannon diversity) and multivariate community metrics (i.e. DCA, SIMPER, etc.) for a more complete picture of how diversity and community structure are interrelated.

Overall, this study is a prime example of how incorporating even very basic habitat data collected alongside fisheries monitoring sampling efforts can help contextualize observed variation in overall catch and demographics resulting in very applicable management implications. Large-scale fisheries monitoring often lacks on-site habitat characterization, specifically with regard to physical habitat. Similar findings were presented by Clarkson & Beseres Pollack (2021), although in that study, the sampling gear used (bag seines) targeted smaller organisms that may be more influenced by local physical habitat. In the present study, larger, wide-ranging species and life stages were similarly linked to local physical habitat at the

site of capture, showing the value of such *in situ* physical habitat data even for wide-ranging specimens. Collection of *in situ* habitat data in Texas is now being incorporated into some fishery-independent resource sampling as a means of including habitat features as variables in future studies.

A final point to be made from this study is in regard to the value of oyster reefs as estuarine habitat. Although previously highlighted in several published studies (e.g. Lenihan 1999, Plunket 2003, Tolley & Volety 2005, Stunz et al. 2010, Beck et al. 2011, De Santiago et al. 2019, La Peyre et al. 2019), the findings here add yet more support to the overall necessity of oyster reef habitat on the estuarine landscape and help discern the complex demographic interactions of estuarine predators, such as spotted seatrout, with oyster reef habitats. While a basic understanding of community- or species-level abundance among habitat types is valuable, species-specific demographic use patterns help us infer possible causation of heterogeneity and are helpful in adding detail as to why such habitats are needed in the landscape and how degradation or complete loss of these habitats may affect the species and populations that rely on them.

From a broader perspective, the ecosystem services provided by oyster reefs have previously been estimated to be high enough as to recover the cost of targeted reef restoration projects in as few as 2 yr (Grabowski et al. 2012), highlighting their ecological value as a competing interest with commercial harvest value. Although they were once a dominant feature of estuaries worldwide, long-term coastal degradation and systemic fishery harvest have resulted in the functional extinction of a majority of the world's oyster reefs (Beck et al. 2011). As more pressure is expected to be placed on coastal habitats from both anthropogenic and environmental sources, assessments of the biological importance of these habitats provide guidance for fishery managers as they attempt to balance these various sources of value with an eye towards ecological sustainability of one of the most important foundation species in the Gulf of Mexico.

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database curated by the Texas Parks and Wildlife Department, and can be made available by request from the Coastal Fisheries science director or the corresponding author. Fish collection and handling protocols were in accordance with ethical guidelines stipulated by a Federal Sport Fish Restoration grant agreement, Texas Parks and Wildlife Department TX F-281-M, as well as a federal permit for the handling of endangered and threatened species issued by the Department of the Interior, permit number TE814933-0.

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