RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Which attributes of restored oyster reefs provide the best habitat for sportfish?

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Abstract

Introduction: Restoration practitioners seek to restore oyster ecosystems as habitat designed for species targeted by recreational fisheries, but they require information on which specific habitat parameters of oyster reefs are preferred by fish.

Objectives: We evaluated the use of restored oyster reefs with a diverse suite of design characteristics (i.e. substrates, depths, and rugosities) by common recreational fisheries species and other fishes that occupy similar habitats. We quantified (1) broad-scale site fidelity of fishes at restored reefs, (2) fish association with particular reefs made from substrates including oyster shell, river rock, limestone, concrete rubble, and mixed shell and concrete poles, and (3) the influence of reef rugosity, edges, and depth on fish preference.

Methods: Fish movements were tracked using surgically implanted transmitters and monitoring their positions using an array of acoustic receivers at restored reefs with different characteristics.

Results: Oyster shell or limestone deployed with high rugosity was preferred by sportfish instead of concrete rubble, river rock, and low rugosity reefs. Red drum (*Sciaenops ocellatus*) preferred shallower reefs (0.5 m) and Black drum (*Pogonias cromis*) preferred deeper reefs (1.0 m). Substrate type has the greatest influence on fish locations followed by depth, then rugosity. Reefs with high perimeter to area ratio may also enhance habitat with fishes most often found associated with reef edges rather than the center of reefs or surrounding sand.

Conclusions: Restoration practitioners can incorporate these design elements to enhance oyster habitat for recreational fisheries.

Implications for Practice: Results can be used by restoration practitioners to design reefs that enhance sportfish habitat. Oyster cultch or limestone substrates deployed with high rugosity and high perimeter to area ratio are preferred over concrete rubble, river rock, and low rugosity reefs. Specific depth zones are preferred by Red drum (approximately 0.5 m deep) versus Black drum and hardhead catfish (approximately 1.0 m). Sand bottom adjacent to reefs is preferentially used by fish compared to other sand regions and could be counted toward goals for area of restored fish habitat.

Key words: biotelemetry, Black drum, depth, edge, habitat partitioning, Red drum, rugosity, substrate

Introduction

Oyster reefs provide habitat for many sportfish targeted by recreational fisheries. Unfortunately, the horizontal extent and vertical structure of oyster reefs are in decline in many regions due to unsustainable and often destructive harvest practices (Beck et al. 2011; Zu Ermgassen et al. 2012). The physical removal of reef structure through mechanical harvest by dredges in particular diminishes their ecological value as fish habitat (Lenihan & Peterson 1998). In response, coastal managers seek cost-effective ways to enhance or restore oyster ecosystems (Peterson et al. 2003; Grabowski et al. 2012; La Peyre et al. 2014). Where oyster larvae are not limiting, restoration is principally done by placing suitable hard substrates in appropriate locations (Beseres Pollack et al. 2012; Brown et al. 2014) for oyster larvae to settle and grow into new or restored reefs that may be utilized by fishes and other organisms (Plunket & La Peyre 2005; Coen et al. 2007; Pierson & Eggleston 2014). Identifying the best substrates, depths, rugosities, and spatial arrangements for oyster reef restoration remains a key information gap to maximize benefits to fishery species.

Author contributions: MSK, LS, KMS, CB conceived and designed the research; MSK, LS, VMC, CB, TAP, BVC, KMS performed the field work; BVC, MSK analyzed the data; MSK, BVC, LS, TAP, KMS, CB, VMC wrote and edited the manuscript.

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doi: 10.1111/rec.70430
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70430/suppinfo

Hard substrates for creating and restoring oyster reefs can include a variety of materials such as old shells, various types and sizes of rocks, and reclaimed concrete structures or rubble (Whitman & Reidenbach 2012; Brown et al. 2014; Dunn et al. 2014; La Peyre et al. 2014; George et al. 2015). These can be deployed in various spatial configurations, thicknesses, and depth zones. Each variable can influence the cost and benefit of restoration projects (Grabowski et al. 2012; Humphries & La Peyre 2015; Graham et al. 2017; Davenport et al. 2021) as fish habitat.

In addition to comparing oyster recruitment and growth among restoration designs, studies often explore the habitat value of restored oyster reefs for the diversity of small fishes and crustaceans that live within the reef structure (Humphries et al. 2011; Humphries & La Peyre 2015; Rezek et al. 2017; Davenport et al. 2021). These relatively sessile organisms are effectively evaluated with small sampling trays (Dillon et al. 2015; Graham et al. 2017; Blomberg et al. 2018), seines, drop samplers, and traps (Brown et al. 2014; Rutledge et al. 2018); however, such methods are easily avoided by larger, more motile fishes such as those targeted in recreational fisheries. Whereas the smaller reef inhabitants are often site-attached once settled onto a reef, questions remain about the site fidelity of larger fishes both at fine scales on particular reefs and over broader scales to restoration areas in general.

Habitat use by these larger fishes is more often assessed using collection methods including nets (Harding & Mann 2001; Plunket & La Peyre 2005; Brown et al. 2014; Pierson & Eggleston 2014; Humphries & La Peyre 2015) which provide snapshots of the transient fish community. However, nets do not provide a measure of how much time fishes actually spend at particular reefs, whether fish are passing through, stopping for a time, or are simply highly mobile residents.

In contrast, tools like passive acoustic telemetry have the advantage of non-destructively tracking fish presence but can be limited in determining the details of habitat preferences in ways that are useful to restoration practitioners. Broad-scale movements are often monitored using an array of widely spaced telemetry receivers throughout an estuary. This has been used to examine fish movements in relation to environmental variables (Dresser & Kneib 2007; Bacheler et al. 2009b; Kendall et al. 2024) or seasonal migrations (Reyier et al. 2011; Hall et al. 2019) at the estuary scale (i.e. 100–1000's of m), but it lacks the spatial precision to identify which specific habitats are preferred. Other telemetry studies have used fine-scale positioning systems to pinpoint fish locations within a few meters on specific bottom features (Dance & Rooker 2015; Moulton et al. 2017). However, even studies that use fine-scale positioning systems have offered limited insight because there are few opportunities to deploy them in experimental settings with a wide range of habitat variables of interest to restoration practitioners.

The goal of this study was to evaluate the use of restored oyster reefs with a diverse combination of design characteristics (i.e. substrates, depths, and rugosities) by common recreational fisheries species and other fishes of similar size (i.e. >20 cm TL) that occupy the same habitat. Fish movements were tracked by implanting acoustic transmitters into them and then monitoring their movements using an array of acoustic receivers and a fine-scale positioning system over a grid of restored oyster reefs with different characteristics. Specifically, we sought to: (1) evaluate broad-scale site fidelity of fishes at restored reefs in general, (2) quantify fish association with particular restored reefs constructed from various substrates, and (3) determine the influence of reef rugosity, edges, and depth on fish preference among reefs.

Methods

Study Location

The study location in Mission-Aransas estuary, Texas, United States (Fig. 1A), is characterized by shallow (<2 m depth), turbid water (approximately 50 NTU) (Rezek et al. 2017; Palmer et al. 2023), that has historically supported recreational fishing communities (Ropicki et al. 2016) and commercial oyster (*Crassostrea virginica*) fishing industries (Martinez-Andrade 2018; Jensen 2020). By 2007, the spatial extent of oyster reefs in the estuary was only approximately 12% of what it was in 1891 (Zu Ermgassen et al. 2012), and recent increases in harvest have elevated concerns for oyster communities and the ecosystem services they provide (Texas Parks and Wildlife Department 2022).

This study focused on a group of 20 oyster reefs constructed in multiple phases on sand bottom in a grid layout off Goose Island (referred to collectively as Goose Island reefs) (Fig. 1B & 1C). These reefs varied based on several physical characteristics that likely influence their value as fish habitat, including substrate type, age, depth, and rugosity. Construction began in 2012 approximately 200 m from shore with four rectangular reefs (approximately 30 by 20 m) composed of a layer of concrete rubble topped with reclaimed oyster shells (Rezek et al. 2017) (Fig. 1C). In 2013, 12 more reefs consisting of three replicates with four substrate types were added, including oyster shell (approximately 9 cm diam.), flint/river rock (approximately 9 cm), limestone (approximately 14 cm), and concrete rubble (approximately 14 cm) (Graham et al. 2017). In 2021, four more were installed seaward of the original grid using recycled concrete construction barriers that were shaped like long poles (approximately 12 m long, approximately 60 cm tall, approximately 60 cm wide). These structures, hereafter called concrete poles, were laid horizontally with an approximately 50 cm wide space in between partially filled with oyster shell (Palmer et al. 2023). To reflect changes in reef extent since their original rectangular shape, edges were digitized from a 2023 satellite image (Esri/Wayback 2023-11-01) (Fig. 1C). These reefs are surrounded by bare sand for more than 100 m in all directions.

Benthic communities (e.g. oyster cover and motile epifauna) have been studied on each reef previously, and oysters readily recruited to them all, but unfortunately there are no recent data for all reefs available to characterize their current status. At the time of the last evaluation in 2021, densities of oysters greater than 25 mm ranged from 150 to 200/m^2 and live oysters covered

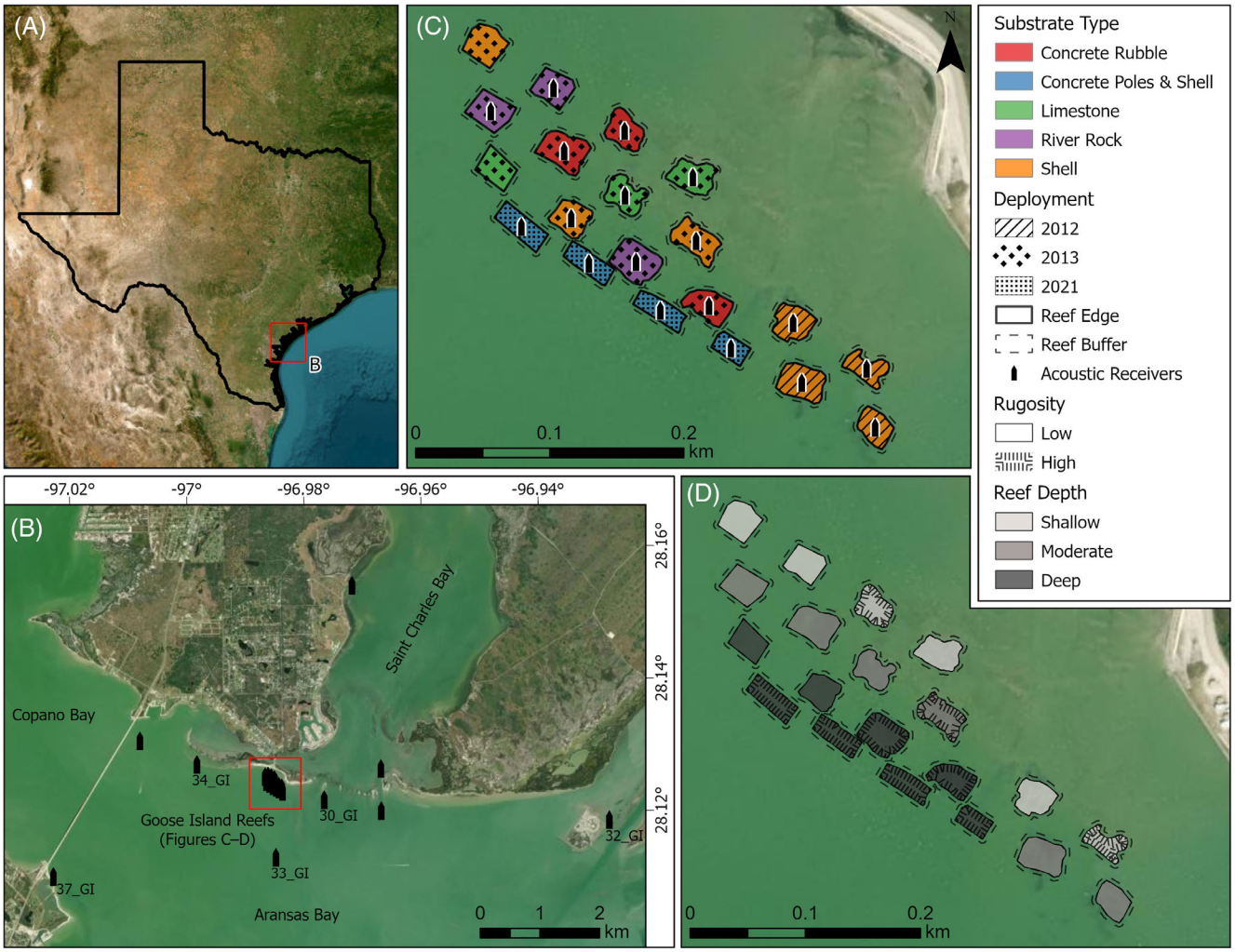

Figure 1. Oyster reef restoration area off Goose Island in Aransas Bay, Texas, United States. Inset maps show (A) the general location of Aransas Bay, Texas, (B) the receiver outer array deployed within Mission-Aransas Estuary with receiver labels for those noted in the text, (C) location of receivers, substrate type, and deployment year for the Goose Island oyster reefs, and (D) rugosity and reef depth characteristics for the Goose Island oyster reefs. *Imagery source*: Esri Wayback, 1 November 2023.

30–50% of the substrate (Palmer et al. 2023). Importantly, however, prior studies at those reefs (Graham et al. 2017; Rezek et al. 2017) and elsewhere revealed that restored reefs of various compositions achieved a benthic community similar to natural reefs within just 4–18 months of restoration (Pierson & Eggleston 2014; Dillon et al. 2015; George et al. 2015; Blomberg et al. 2018). Given that all these reefs were at least 2 years old when the present study took place, the year of establishment was not included in the analyses. In contrast, reef rugosity (i.e. variation in height) was quite different among reefs. Most were initially created with a consistent approximately 30 cm vertical height above the surrounding substrate except for the approximately 60-cm tall concrete poles. However, bioerosion, oyster accretion, storms, or other factors altered their vertical profiles. A consistent estimate of rugosity among reefs was created based on 20 haphazard depth measurements on each reef. These were taken at the conclusion of the tracking period using a weighted measuring tape. Standard deviation of depth was used to represent relative rugosity. Reefs were classified along a natural break in the distribution as high (10–14 standard deviation SD of depth measurements, 40 cm depth range) or low rugosity (3–8 SD, 20 cm range) (Fig. 1D).

Water depth in this area gradually slopes such that we categorized the six reefs closest to land as shallow (approximately 90 cm deep), the eight farthest from land as deep (approximately 115 cm deep), and the six in between as moderate depth (approximately 102 cm deep) (Fig. 1D). Variations in overall depth depend primarily on wind forcing (mean diurnal range = 0.11 m, https://tidesandcurrents.noaa.gov).

Fish Tracking

Species targeted here included Black drum (*Pogonias cromis*), Red drum (*Sciaenops ocellatus*), Spotted seatrout (*Cynoscion nebulosus*), Hardhead catfish (*Ariopsis felis*), Gafftopsail catfish (*Bagre marinus*), and Southern stingray (*Hypanus americanus*)

(Table S1). These are important in recreational fisheries, regionally abundant, and have suspected associations with oyster reef ecosystems (Patillo et al. 1997; George 2007; Brown et al. 2008; Moulton et al. 2017). From 26 April to 1 May 2023, fish were caught on or adjacent to the 20 study reefs using hook and line. Minimum size for tagging was 20 cm total length (TL). A coded transmitter (InnovaSea Inc. model V8-4L, 130–230 s ping interval, 405 day battery) was inserted into the body cavity of each fish through a 1.5 cm ventral incision (Reese Robillard et al. 2015), and fish were released at the point of capture following the approximately 2-minute procedure.

Fish movements were monitored for 1 year beginning in May 2023 using a multi-scale array of automated acoustic receivers affixed to plastic poles. Broad-scale movements outside of the Goose Island reefs were monitored by a widely spaced array of nine receivers (InnovaSea Inc., model VR2W), hereafter referred to as the outer array (Fig. 1B). These were placed at suspected movement corridors leading away from the Goose Island reefs. Precision of fish positions within the outer array was limited to the approximately 100–150 m detection range of the receivers. For the Goose Island array, fine-scale locations (i.e. within a few meters) on the oyster reefs were determined using an array of 20 receivers (InnovaSea Inc., model VR2Tx) deployed in the middle of each of the study reefs (Fig. 1C). At the end of the tracking period, data were downloaded and time corrected for internal clock drift. All analyses were conducted in R (Version 4.4.1).

Data Analysis

Broad-Scale. To determine how much time fish spent at Goose Island reefs versus moving more broadly in the estuary in the outer array, the days with detections were plotted from the date fish were tagged until their transmitter batteries expired. Those detection days (DD) were categorized by location: only at the Goose Island array, only on the outer array, or on both on the same day. Proportions of each fish's total DD among those three categories were summarized and used to calculate average values for each species. Patterns of specific receivers used by fishes on the outer array and synchronous seasonal timing of movements were noted. Dates with synchronous movements were compared to water temperature (National Oceanic and Atmospheric Administration NOAA station ID8774230).

Fine-Scale. Fine-scale fish positions were triangulated using Fathom Position software (InnovaSea Inc.) based upon time of signal arrival at Goose Island reef receivers. Because each position includes an estimate of horizontal-positioning-error, unacceptable data can be filtered out (Smith 2013; Meckley et al. 2014). Balancing the requirement of precision to meet study objectives (i.e. linking fish positions with specific reefs) while minimizing data loss, a maximum allowable error of 5.7 m (median 1.6 m) from actual fish positions was used to filter the data. This reduced the data for analysis by 43.6%. In addition, positions more than 21 m from the outside edge of the outermost reefs were excluded since those fish were outside the immediate vicinity of the Goose Island reefs and not relevant for identifying fish preferences among reef types. This distance was selected because it was greater than the maximum space between reefs. This reduced the number of positions by another 1.4%. Lastly, fish with fewer than 25 positions at Goose Island were also removed from analysis. Collectively, these steps eliminated fish with too few datapoints, those datapoints lacking sufficient accuracy to meet study objectives, or those too far from study reefs to meet objectives. Number of unique days positioned, and proportion of days positioned on the Goose Island array compared to the total tracking span (i.e. days between tagging and date of last position in the Goose Island array) were summarized for each individual.

Preliminary evaluation of positions revealed that many were located directly on top of specific reefs, but also along the edges of reefs (Fig. 2). We therefore sought to quantify the relationship between fish positions and reef edges. Specifically, it was of interest to determine whether fish positions relative to reef boundaries differed from random positions, and if so, how far from a reef edge a fish position should still be considered as associated with a particular reef.

For this analysis, the distance from each fish position to the nearest reef edge was calculated (*sf* package; Pebesma 2018) and saved as a positive value for locations outside the reefs (i.e. in the surrounding sand) and a negative value for locations inside (i.e. on the reef). The number of distance values for each fish was then summed within 1 m bins at increasing distances beginning on the reef edge (i.e. from −0.5 to +0.5 m of the edge), and extending inside (−0.5 to −1.5, −1.5 to −2.5 m, etc.), and outside of the reefs (+0.5 to +1.5, +1.5 to +2.5 m, etc.), and plotted as a histogram. Histograms for each fish were then standardized as the proportion of position counts within each distance bin. Then for all individuals of each species, the mean (± SE) proportion of positions in each distance bin was calculated such that a single histogram for each species summarized their location patterns relative to reef edges.

We then used these histograms to determine if fish positions relative to the reef edge were significantly different from random movements. For this analysis, we took the number of positions observed for each real individual and generated the same number of randomly positioned points within the Goose Island array. As was done for the observed positions, the distance from reef edge was calculated for each random point and used to create a histogram. Kolmogorov–Smirnov tests were used to determine if the observed histogram for each species was significantly different from the random histogram.

The next part of the analysis tested whether each species was preferentially using one reef substrate versus another and what other factors (i.e. depth and rugosity) might have influenced reef use. For this analysis, each fish position was assigned to an individual reef if the fish's location was either inside that reef polygon, or within a species-specific buffer zone surrounding it. Buffer width was based on natural inflection points in the observed histograms of fish locations relative to reef edges, such that 75% of all positions for each species were associated with reefs. This value incorporated a large majority of animal position counts including all positions that occurred on or adjacent

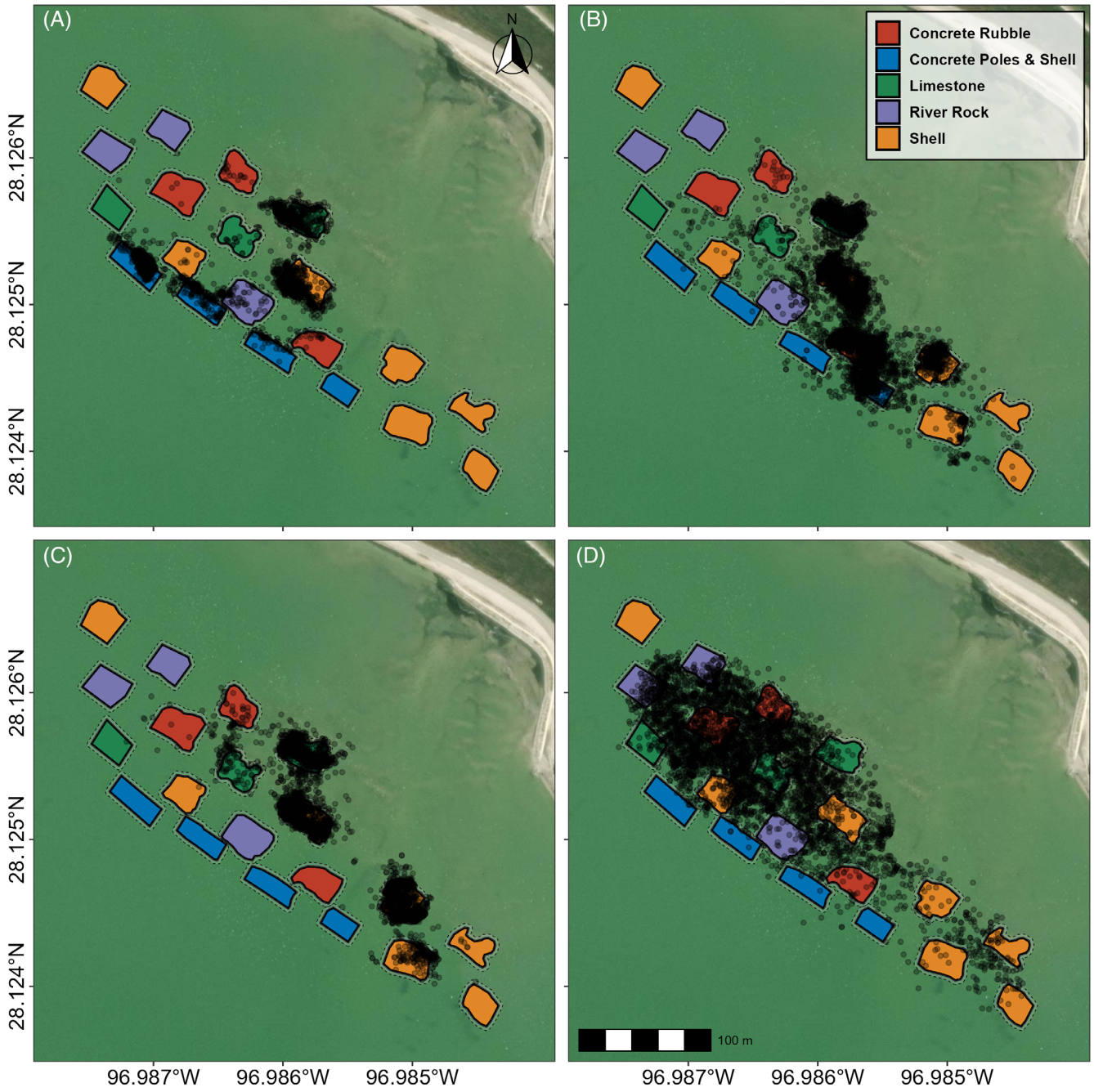

Figure 2. Representative plots of detection positions that met minimum HPEm criteria from an individual (A) Black drum (POCR-547), (B) Hardhead catfish (ARFE-573), (C) Red drum (SCOC-665), and (D) Southern stingray (HYAM-666).

to the reef but excluded the 25% of positions in the tail of the distribution furthest out into the sandy spaces surrounding reefs. In cases where reefs were close together and the buffer zones overlapped (e.g. most concrete poles and shell reefs), the buffers were split equally. All positions that fell in the open sandy areas between or beyond the buffers were excluded. After these steps, remaining fish positions were associated with their closest study reef.

A generalized linear mixed (GLM) model (*glmmTMB* package; Brooks et al. 2017) was used for each species to identify reef preferences. The number of positions at each reef were tallied hourly for each fish, with any reefs where an individual was not positioned receiving a tally of zero. These values served as our proxy for reef preference. Variables that may contribute to fish preference for a reef were examined, including fixed effects of substrate type (i.e. concrete rubble, concrete poles and shell, limestone, river rock, and shell), reef depth (i.e. shallow, moderate, and deep), and rugosity (i.e. high and low); a random intercept effect for each fish (to account for potential intraspecific variation); and a first-order autoregressive error structure by

time, grouped by fish, to account for spatial and temporal autocorrelation. Additionally, because some substrates covered more area than others, a log offset for total substrate areas was evaluated. All model components were checked for collinearity using variance inflation factors (Zuur et al. 2010), which were all less than 10, so all components were kept in the models. Zero-inflation and overdispersion were investigated using the *DHARMa* package (Hartig 2024). Appropriate model likelihood distributions tested included Poisson, negative binomial, generalized Poisson, and Tweedie, and were selected based on the lowest Akaike's Information Criterion (AIC) and visual inspection of diagnostic plots from the *DHARMa* package. Model selection was conducted using the dredge function of the *MuMIn* package (Bartoń 2025) whereby the random effect of individual ID and the spatiotemporal autocorrelation term were included in all model iterations. The best model was determined from the lowest AIC value. We then plotted the marginal mean estimates of the number of hourly positions predicted from the GLMs (*emmeans* package, Lenth 2025). Marginal means estimates predict the size and strength of the effects of each variable in isolation while accounting for the average or most common conditions of all other variables across the reefs. Tukey's post hoc pairwise comparisons were conducted to identify significant differences among factor levels for relevant variables. Although the study reefs did not consist of a full factorial design (i.e. concrete poles were only in the deeper areas and inherently cannot have low rugosity), there was sufficient overlap in combinations of reef attributes to enable analysis of all reefs together. In cases where results depended on reefs with attributes that were potentially confounded, additional analysis of reef subsets were undertaken without those variables to confirm that results from the whole model were robust.

Results

A total of 55 fishes were tagged including 20 Spotted seatrout, 13 Black drum, 9 Red drum, 5 Gafftopsail catfish, 5 Hardhead catfish, and 3 Southern stingrays. The number and duration of detections in both arrays varied widely among species (Fig. 3). Most Spotted seatrout and Gafftopsail catfish had few or no detections at the Goose Island reefs, and were only detected in the outer array for a few weeks. Therefore, only broad-scale movements were evaluated for those two species. The other four species had much longer detection spans at Goose Island. All but one Red drum and five Black drum were detected at Goose Island reefs for 5–7 months. All of the Hardhead catfish and two of the Southern stingrays had very robust detection records with almost daily detections except during winter months.

Broad-Scale Movements

Overall, 46 individuals were detected on the outer array, including all Hardhead and Gafftopsail catfish, Spotted seatrout, and Southern stingray (Table S1). In contrast, only nine of 12 Black drum and four of nine Red drum were detected on the outer array. The average number of DD for fish on the outer array was 11 (±3 SE) days (0–142 day range). Gafftopsail catfish had the largest percentage of their total DD on the outer array (81% ± 19), followed by Spotted seatrout (80 ± 5), Black drum (37 ± 14), Southern stingrays (21 ± 20), Red drum (9 ± 5), and Hardhead catfish (7 ± 3). There were no consistent species-specific location patterns for fish on the outer array. The three receivers visited by the most individuals ($n = 27$ at 30_GI, 25 at 34_GI, and 23 at 33_GI) were those closest to the Goose Island reefs, whereas receivers farthest from Goose Island detected the fewest ($n = 5$ at 32_GI, and 6 at 37_GI). Because the Gafftopsail catfish and Spotted seatrout quickly left the Goose Island reefs and had few positions there, they were excluded from fine-scale analysis.

There were some species-specific seasonal patterns in detections (Fig. 3). All five Hardhead catfish departed the Goose Island array on 27 November 2023, at the same time as a cold front reduced water temperatures from 17 to 12°C. They returned to the Goose Island array regularly once water temperatures rebounded above approximately 20°C in February–March 2024. Two of the Southern stingrays also exhibited fewer detections at the Goose Island array during winter months, especially late January, before returning consistently to Goose Island in February when water temperatures increased. The Gafftopsail catfish and Spotted seatrout nearly all departed the area soon after tagging in May, coincident with daily water temperatures increasing above 24°C. Black drum also exhibited some seasonal patterns, although the response was mixed such that on 21 November 2023, four shifted away from the Goose Island array whereas two others increased their occupancy at Goose Island. This date corresponded to a cold front with a temperature drop from 21 to 15°C. Lastly, several of the Red drum departed the Goose Island array in late October 2023 although water temperature showed no anomalous values around those dates.

Fine-Scale Locations

Four Back drum and two Red drum had fewer than 25 positions within the Goose Island reef array and were excluded from the fine-scale analysis. The remaining individuals including five Hardhead catfish, three Southern stingrays, eight Black drum, and seven Red drum underwent fine-scale positioning analysis over the Goose Island reefs. Hardhead catfish had the most consistent use of the Goose Island reefs compared to the other species with a tracking span ranging from 163 to 280 days (219 days ±19 SE). This corresponded to 47–77% of their total detected days (60% ± 10 SE; Table S1). Southern stingrays had the second highest number of days positioned (189 days ±91 SE) and were detected on 66% (±10) of days during the tracking period. Black drum were positioned at Goose Island over an average of 117 days (±29 SE) during the tracking span corresponding to 41% (±11 SE), followed by Red drum with an average of 49 days (±29 SE), or 26% (±8 SE) of their tracking span. Collectively this indicates regular occupancy and high site fidelity of Goose Island reefs for these species to enable fine-scale positioning analyses.

The histograms of fish positions relative to reef edges indicated that fish were not using the area randomly (Kolmogorov–Smirnov $p < 0.05$) (Fig. 4). Most Hardhead

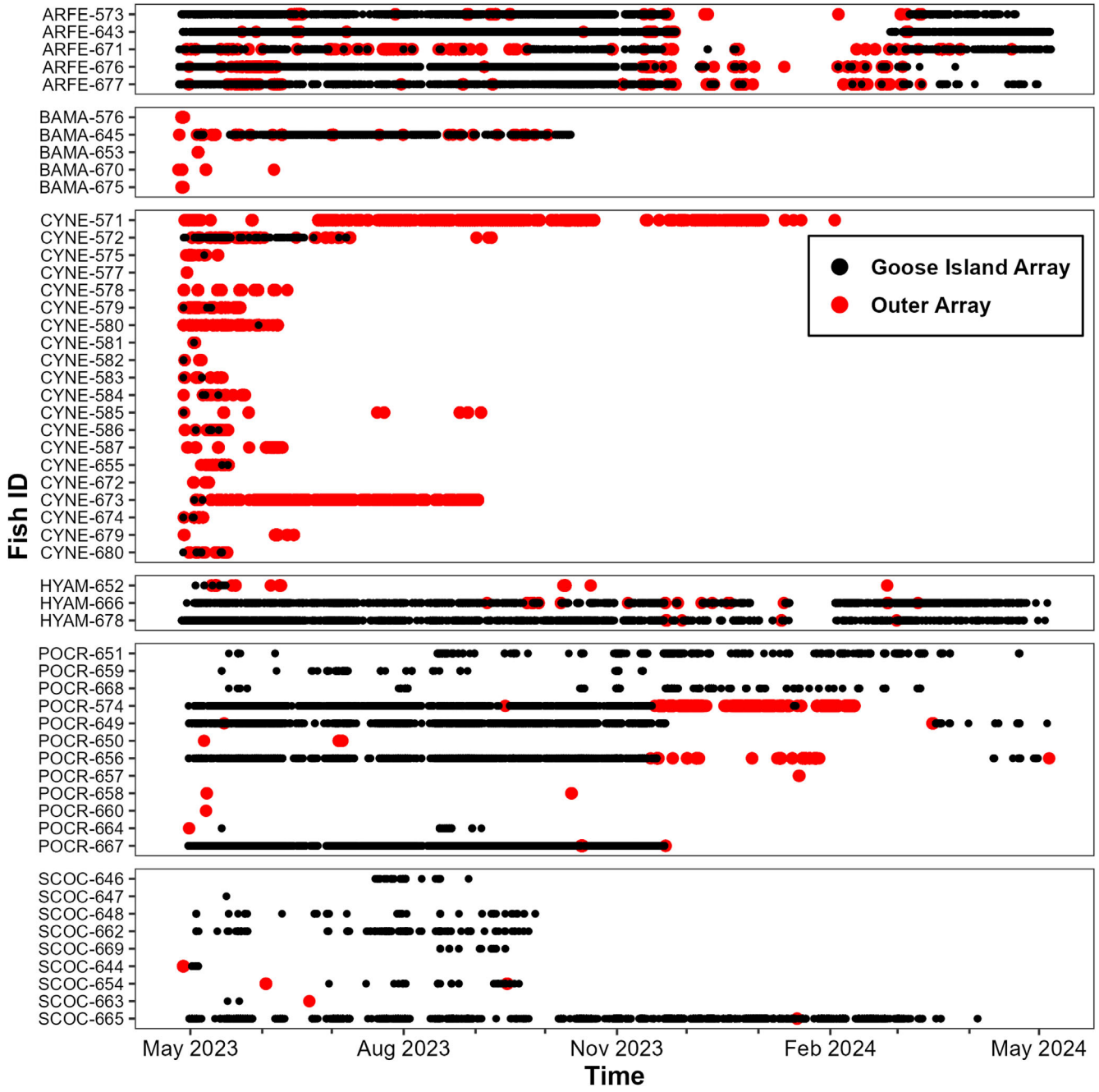

Figure 3. Abacus plot of detection days at the Goose Island oyster reefs (black points) and the outer array (red points). Individual fish are labeled by transmitter number and species. Species codes are Hardhead catfish (ARFE), Gafftopsail catfish (BAMA), Spotted seatrout (CYNE), Southern stingray (HYAM), Black drum (POCR), and Red drum (SCOC).

catfish positions were on top of reefs, with a mode of 2–3 m inside the reef edge (Fig. 4B) and 75% of their positions on top, or within 1.1 m of reef edges (Fig. 4B). The mode for Black drum was most directly associated with the reef edge (i.e. most positions were in the −0.5 to +0.5 m analysis bin) and 75% of their detections were on top, or within 3.1 m of reef edges (Fig. 4A). Red drum positions had a mode just outside the reef but were still highly associated with the edge (i.e. +0.5 to +1.5 m bin), with 75% of positions occurring on top, or within 1.5 m of reef edges (Fig. 4C). For these three species which were associated with reef edges, the outline of individual reefs was visible by plotting fish positions (Fig. 2A–C). Based on the 75th percentile, buffer widths of 3.1, 1.1, and 1.5 m from the outside edge were used for Black drum, Hardhead catfish, and Red drum, respectively, when assigning fish to individual reefs for the GLM analysis. In contrast, Southern stingray distribution

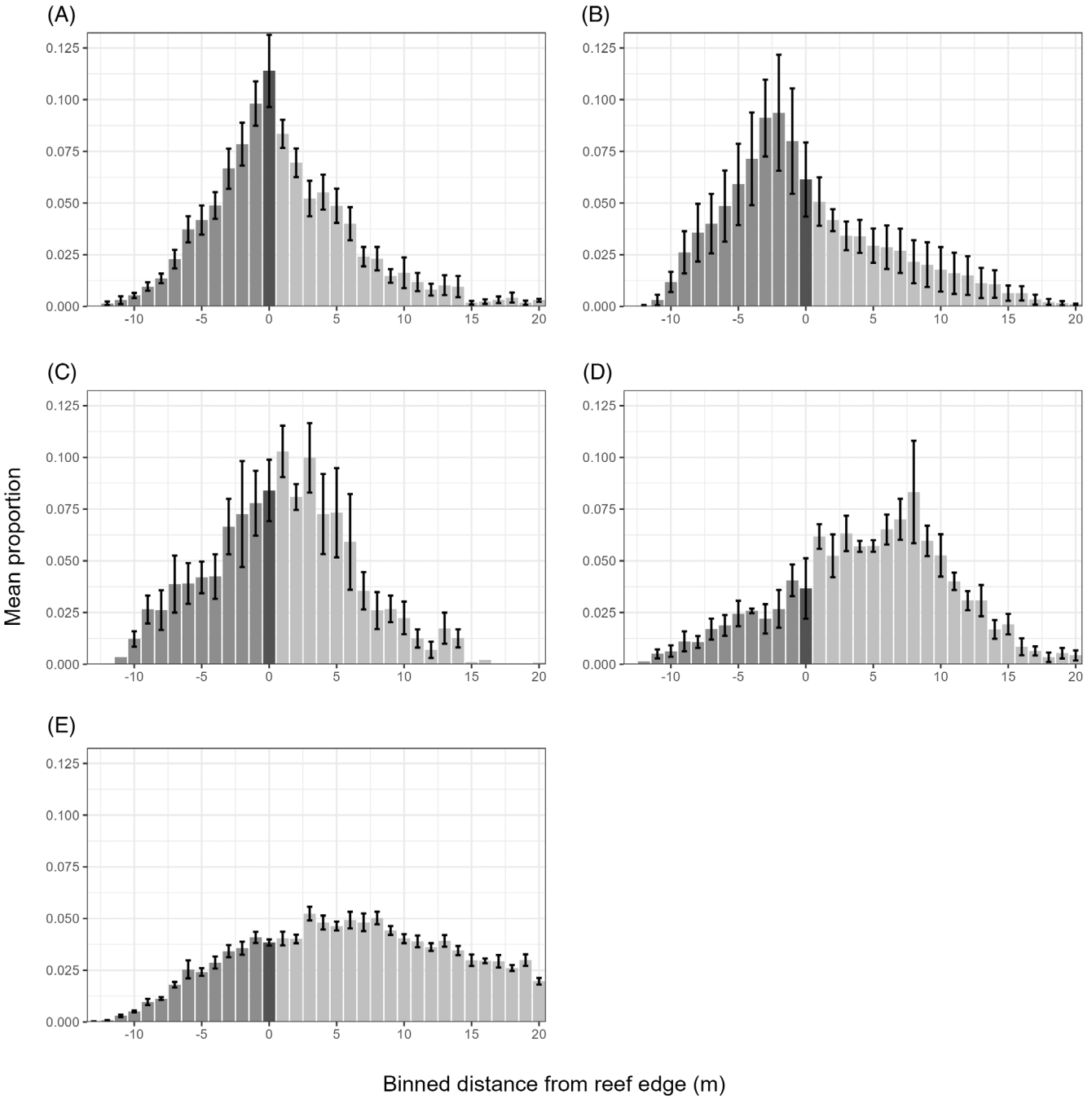

Figure 4. Histograms of the mean (± SE) proportion of fish positions for each species relative to their distance from the reef edge (i.e. Dark gray bar at distance = 0) for (A) Black drum, (B) Hardhead catfish, (C) Red drum, (D) Southern stingray, and (E) random. Distance bins inside the reef edge are negative and shaded medium gray on the left side of each panel. Distance bins outside the reef edge are positive and shaded light gray on the right side of each panel.

was similar to random on top of reefs. The mode for their positions was 8 m outside the reefs with most of their positions occurring in the sand between reefs before dropping off 10–15 m away from the edge (Fig. 4D). Since association with reefs was similar to random and the majority of Southern stingray positions occurred in the sand, they were excluded from the analysis identifying reef preference.

The species-level models revealed differences among species in their utilization of various reef substrates, depths, and rugosity. For all species, the top two models were within a ΔAIC of 2 and had similar model weights, with the only difference being the inclusion of the substrate area offset. Given its small influence, and to have the most parsimonious model, the offset term was removed from all models.

All explanatory variables were included in the best model for Hardhead catfish. Number of Hardhead catfish positions per hour was significantly different among all reef substrates ($p < 0.01$), with shell having the most ($p < 0.001$) (Fig. 5A). Deeper reefs had significantly more fish positions than shallow ($p < 0.001$) or moderate ($p < 0.001$) reefs (Fig. 5B). High rugosity reefs had significantly more fish positions than low rugosity reefs ($p < 0.001$; Fig. 5C), although effect size was an order of magnitude smaller than for depth or substrate type.

Similarly, the best model for Red drum consisted of all explanatory variables. Limestone had significantly more Red drum positions than all other material types ($p < 0.001$), followed by shell ($p = 0.001$). Concrete poles and shell had the third most positions but were not significantly different from concrete rubble ($p = 1.000$) or river rock ($p = 0.531$) (Fig. 5D). Red drum had significantly more fish positions on shallow reefs than moderate ($p < 0.001$) or deep reefs ($p < 0.001$; Fig. 5E). Additionally, higher rugosity reefs had significantly more fish positions than lower rugosity reefs ($p < 0.001$; Fig. 5F), although again the effect size was much smaller than the other variables.

Lastly, the ideal model for Black drum only included reef substrate and depth as explanatory variables but not rugosity. All material types were significantly different ($p < 0.001$), but Black drum had significantly more positions on concrete poles and shell reefs compared to all other reef types ($p < 0.001$), followed by shell, limestone, river rock, and then concrete rubble (Fig. 5G). Deeper reefs had significantly more Black drum positions than shallow ($p < 0.001$) or moderate depth reefs ($p < 0.001$, Fig. 5H). Since all four concrete poles and shell

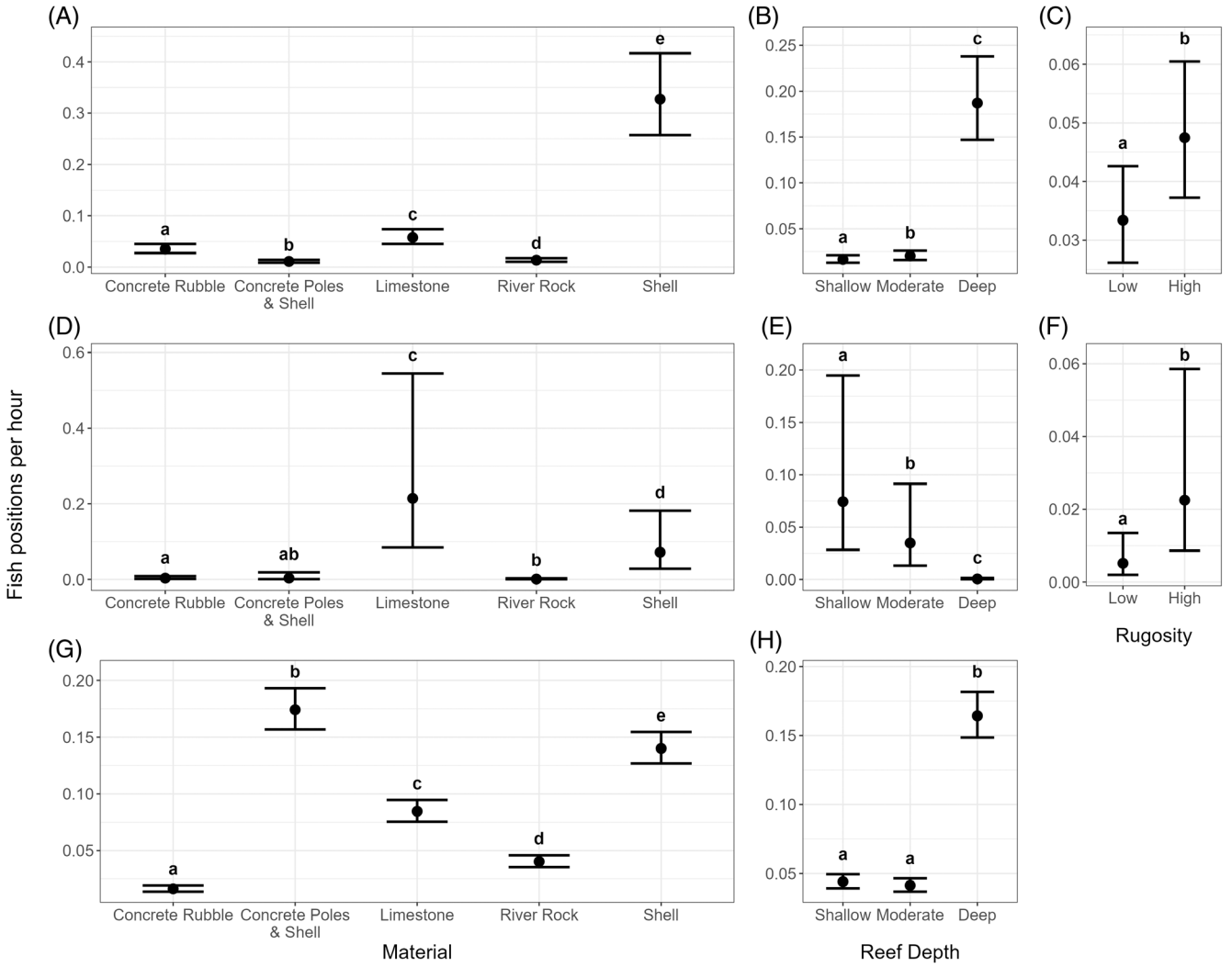

Figure 5. Predicted number of fish positions per hour (± 95% CIs) from the GLM for variables included in species-specific models. The ideal models for Hardhead catfish (A–C) and Red drum (D–F) both included material, reef depth, and rugosity, whereas the ideal model for Black drum (G, H) only included material and reef depth. Letters denote significant differences ($p < 0.05$) within subfigures. Best fitting data distribution types for these GLMs were Tweedie with a log link function for Hardhead catfish, a generalized Poisson with a log link function for Black drum, and a negative binomial distribution with a log link function for Red drum.

reefs were in the deep category, and those two variable levels were preferred by Black drum, we conducted two supplemental analyses on two reef subsets to confirm that results based on analysis of all the reefs together were robust. In one analysis, concrete poles and shell reefs were excluded and the outcome was the same as in the results presented in Figure 5H where deep reefs were the preferred depth stratum for Black drum. In another analysis, only the eight reefs in the deep stratum were analyzed and again, the outcome was consistent with Figure 5G wherein Black drum preferred concrete poles and shell and shell substrates. There were other statistically significant differences among some factor levels for these species (Fig. 5); however, the actual differences were small, unlikely to be ecologically meaningful, and were therefore not highlighted.

Discussion

Tracking fish locations among the restored Goose Island oyster reefs provided an ideal opportunity to evaluate fish preferences among multiple reef substrates, depths, and rugosities to inform future oyster reef restoration. Overall, results suggest that either oyster shell or limestone substrates that are deployed with high rugosity are preferred substrates over concrete rubble, river rock, and low rugosity reefs. Sportfish were also primarily associated with reef edges suggesting that high perimeter to area ratio (i.e. lots of edge per unit area) may further enhance reef habitat. Restored reefs in all depth zones evaluated provided habitat. Restoration practitioners can use these findings to design reefs that enhance fish habitat for recreational fisheries.

Although results vary depending on locality, studies investigating multiple substrate types broadly find that oyster shell, concrete, and limestone are equivalent or superior to other substrates in terms of oyster recruitment and as habitat for small motile fauna (Brown et al. 2014; George et al. 2015; Graham et al. 2017). Results here indicate that restoration substrates that include shell or limestone as the top layer had four to eight times higher prevalence of fishery species than other substrates and should be given priority to maximize fishery benefits. There are, of course, other location-specific considerations when selecting substrates depending on factors such as the potential for future oyster harvest, boring sponge prevalence, material availability, and costs (Dunn et al. 2014; Graham et al. 2017). It is also important to note that not only were some substrates clearly preferred, but the influence of substrate on fish location was much stronger than that of depth or rugosity. Understanding the relative influence among these three variables is an important aspect of determining the cost–benefit among restoration designs.

Although less influential than substrate type, each species also had preferences for specific depths, with Red drum mostly occupying shallower reefs (approximately 0.9 m deep) and Black drum and Hardhead catfish on deeper reefs (approximately 1.15 m). Each species may best exploit preferred prey at certain depths due to specialized foraging capabilities (Grubich 2005; Brandl et al. 2020), higher abundance of preferred prey at a certain depth (Davenport et al. 2021), or perhaps they partition depth zones to avoid interspecific competition for similar prey (Pekcan-Hekim et al. 2016; Moulton et al. 2017). Whatever the cause, results indicate that restoration can target specific depth zones to preferentially benefit particular species for fishery enhancement.

Although less influential than substrate or depth, high rugosity reefs were preferred by Red drum and Hardhead catfish. High rugosity provides more niche spaces for a variety of organisms. This increases prey density and diversity for benthic feeding fish including those studied here. Amount of relief also influences the specific types of nekton prey that recruit to reefs (Davenport et al. 2021), which may in turn affect reef choice by predators specializing on those prey. Although the effect size on our fish positions was small, high rugosity has added benefits for reasons besides fish habitat. Taller, more rugose reefs not only have higher oyster recruitment and growth due to higher flow and more turbulence (Lenihan 1999; Whitman & Reidenbach 2012), but they are often elevated above smothering height in regions where sedimentation is of concern. It is important to note, however, that reef height (i.e. maximum elevation above surrounding substrate) and reef rugosity (i.e. surface roughness or variation in reef height) are not interchangeable values. High rugosity promotes habitat variation in a way that differs from a tall but otherwise smooth sided and low rugosity reef. Both properties are likely important in enhancing different aspects of reef habitat. From a cost perspective, achieving higher rugosity by deploying variable thicknesses of hard substrate has the tradeoff of restoring less two-dimensional area (e.g. oyster cultch must be piled higher to meet rugosity goals rather than spread thinly over a larger area). Results here suggest that techniques that combine substrate types may yield the least cost per unit area. Using cheaper, more readily available substrates as a base layer to achieve the rugosity objective, such as deploying an irregular thickness of concrete rubble, and then adding a surface layer of shell on top to achieve the preferred substrate goals, would be more cost effective. In addition, unless the site is intended for future harvest, occasional use of very large rocks or other three-dimensional structure such as the concrete poles used at Goose Island, would provide the added benefit of deterring commercial oyster dredges which can be damaged if snagged on such obstructions.

Due to the high resolution of the position data, it was also clear that reef edges were more heavily utilized by both drum species and Hardhead catfish than either the surrounding sand or even the center of oyster reefs (George 2007). Some fishes focused their activity directly on the reef edge (i.e. Black drum), whereas others utilized the inside edge on the top of the reef (i.e. Hardhead catfish), or the edge just off the reef (i.e. Red drum). As with partitioning habitats based on depth, each species may use slightly different edge space to avoid competition (Moulton et al. 2017), to specialize on micro-habitat that optimizes foraging (Brandl et al. 2020; Hogan et al. 2022), or to conserve energy in preferred resting locations in the flow eddies along reefs (Smith et al. 2014; Pekcan-Hekim et al. 2016). Regardless of the reason, reef edges are clearly preferred, and restoration designs could maximize fish habitat by including high perimeter to area ratio. These results also indicate that restoration practitioners could justifiably consider including a buffer around restored reef patches in their calculations of area

of restored fish habitat with buffer width depending on the species. The sand areas around reefs are functioning as fish habitat in a way that is clearly different from open sandy areas elsewhere, potentially similar to the halo effect seen in soft bottom habitat surrounding other structure types (Kendall et al. 2003; Lytle 2020).

Even species such as Southern stingrays may preferentially select sand areas near oyster reefs rather than using the reefs themselves or sand areas indiscriminately. Durophagous rays are suspected pests of shellfish enhancement activities (i.e. aquaculture and restoration; Merriner & Smith 1979). For example, some rays exhibit extended occupancy of clam aquaculture sites (Cahill et al. 2023). Given the generalist diet of Southern stingrays (O'Shea et al. 2020) and their propensity for the sandy areas near reefs, it is possible that they are benefiting from prey enrichment adjacent to oyster reefs (D'Amours et al. 2008; Hogan et al. 2022).

Although caught on or near the oyster reefs, Spotted seatrout and Gafftopsail catfish quickly left the Goose Island reefs and could not be linked with restoration variables. Potential reasons why they departed the area include the disturbance of tagging, large home range beyond the Goose Island reefs, or environmental cues. Little is known about Gafftopsail catfish movements, but several studies offer insight into Spotted seatrout. For example, summer emigration of Spotted seatrout from estuaries has been observed elsewhere when water temperatures exceed 24°C (Callihan et al. 2013, Tinhan et al. 2018). Indeed, most Spotted seatrout left the Goose Island reefs soon after tagging in May, when temperatures regularly exceeded that value. Two other tracking studies elsewhere in Texas also noted that spotted seatrout generally had low residency, with many individuals leaving those study areas within a few weeks of tagging (Moulton et al. 2017; Tinhan et al. 2018). Those studies also demonstrate that Spotted seatrout are primarily associated with deeper (1–2 m) seagrass habitat rather than shallower oyster reefs.

Seasonal departure of other fish species from the Goose Island reefs was also consistent with prior studies, although the fine-scale positioning of our array enabled deeper insights. For example, Hardhead catfish are thought to move into deeper water to overwinter and return to estuaries in the spring (Patillo et al. 1997), but it was not known that they return to the same particular reef location until this study. Similarly, Black drum used the same parts of a Texas estuary complex for weeks or months before shifting to another location in winter (Ajemian et al. 2018), coincident with lower temperatures and seasonal spawning (Nieland & Wilson 1993). Some Black drum then returned to the same estuary the following spring (George 2007), with our results showing this can be the same exact reefs. Larger Red drum than those in our study were tracked leaving a nearby bay in October and November, somewhat associated with a temperature drop (Hall et al. 2019). Although the temperature relationship was not observed at Goose Island, a fall departure is consistent with the known spawning migration season for that species (Patillo et al. 1997; Reyier et al. 2011). All Red drum tracked at Goose Island, however, were likely subadults based on size (Murphy & Taylor 1990) and may have simply undertaken the periodic home range relocations documented for this species elsewhere (Kendall et al. 2024). None of the Red drum that left in September returned to Goose Island in later seasons.

Among the species studied here, Red drum have received the most attention using acoustic tracking to evaluate their movements. Prior studies have focused on movements in relation to salinity (Bacheler et al. 2009a; Kendall et al. 2024), tides (Dresser & Kneib 2007), temperature (Hall et al. 2019), spawning (Reyier et al. 2011), and other broad-scale activity. They have primarily been conducted with widely spaced receivers similar to our outer array, or are based on intermittent relocations, resulting in coarse resolution poorly suited for identifying specific habitat associations. A couple exceptions that used fine-scale-positioning systems, found Red drum commonly associated with habitat edges, sand, and seagrass (Dance & Rooker 2015; Moulton et al. 2017). Interestingly, they found mixed results for Red drum association with oyster reefs. This disparity could be because one study had very little oyster reef in their telemetry array or their particular reef was of relatively low quality or in a poor landscape setting (Dance & Rooker 2015; Fodrie et al. 2015).

With many oyster reefs at a fraction of their historical extent (Beck et al. 2011; Zu Ermgassen et al. 2012) and growing interest in restoring their ecosystem services (Coen et al. 1999; Stunz et al. 2010; Texas Parks and Wildlife Department 2022), results here and in other studies can be used to maximize the value of restored reefs as habitat for some recreational fisheries. To broaden the scope of these recommendations, it is important that the results here be considered in other landscape settings, depth zones, reef configurations, and seasons. Future restoration studies would also benefit from a full factorial design where all habitat variables are present in every combination. Lastly, it is important to note that although the positioning system used here reveals where fish are, it does not reveal what they are doing. Additional research is needed to inform whether fish are using different parts of the reef for feeding, traveling, or resting. Discriminating among those activities could further enable oyster restoration practitioners to design reefs that promote specific aspects of reefs as fish habitat.

Acknowledgments

J. Pollack and G. Stunz helped guide project conception. Coastal Conservation Association CCA, J. Blaha, Flatsworthy, B. Trimble, C. Naiser, and K. Simms donated fishing days. K. Capistrant-Fossa, B. Batterton, and P. Souza provided field assistance. A. Winship, B. Williams, S. Lombardo, M. O'Brien, and C. Goetsch provided analysis suggestions. A. Winship and B. Williams reviewed a draft manuscript. TPWD Scientific Research Permit SPR-0423-046. Animal care, receiver deployment, and other environmental impacts were approved under the National Environmental Policy Act NEPA, NOAA Administrative Order (NAO) 216-6A. Labor was provided by CSS Inc., under contract GS-00F-217CA/EA133C17BA0062. The authors declare no conflicts of interest. The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Data summaries for tracked fishes including total length (TL), detection days (DD), tracking span in days, and Goose Island (GI) positions.

Coordinating Editor: Philline zu Ermgassen

Received: 15 December, 2025; First decision: 7 March, 2026; Revised: 16 April, 2026; Accepted: 26 April, 2026