



Linking Habitat Use and Trophic Ecology of Spotted Seatrout (*Cynoscion nebulosus*) on a Restored Oyster Reef in a Subtropical Estuary

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Abstract

Predicting population- and ecosystem-level benefits of habitat restoration minimally requires an understanding of the link between the trophic ecology of a species and their use of a habitat. This study combined novel, non-lethal natural tracers of trophic ecology with acoustic tagging techniques to examine spatial and temporal patterns of habitat use of spotted seatrout *Cynoscion nebulosus* on Half Moon Reef (HMR), a recently restored oyster reef in Matagorda Bay, Texas. Forty-one spotted seatrout (408 ± 25 mm total length) were captured at HMR, surgically implanted with acoustic transmitters, and monitored by an array of underwater listening stations from December 2015 to August 2016. Patterns of presence-absence on HMR were strongly influenced by water temperature, and to a lesser extent, salinity and tidal height. Overall, spotted seatrout residency to HMR was low, with fish being present on the reef 24% of days. When present, individual fish exhibited strong site-attachment to small portions of the reef. Residency to HMR increased significantly with size, while scale stable isotope analysis revealed fish exhibiting high residency to HMR occupied significantly smaller isotopic niches. If indeed smaller fish with decreased residency rely upon a wider range of prey items across multiple habitats than larger, more resident individuals, restored oyster reef habitat may be expected to primarily benefit larger spotted seatrout.

Keywords Gulf of Mexico · Acoustic telemetry · Stable isotope analysis · Environmental drivers · Residency

Introduction

Oyster reefs play an important role in the function and resilience of estuarine and coastal ecosystems. Oyster reef habitat can provide a range of ecosystem services, from increased species diversity and trophic interactions via high habitat complexity to localized improvements in water quality driven by oyster filtration (Coen and Luckenbach 2000; Peterson and Lipcius 2003;

Grabowski and Peterson 2007; Beck et al. 2011). However, a combination of anthropogenic alterations to coastal habitat and overexploitation through commercial oyster fisheries have reduced oyster reef coverage in coastal ecosystems (Beck et al. 2011; Wilberg et al. 2011; zu Ermgassen et al. 2012). Restoration of oyster reef habitat has been prescribed as a means of both mitigating coastal habitat loss and enhancing local fisheries (Peterson et al. 2003; zu Ermgassen et al. 2016). Several studies have highlighted the importance of oyster reef habitat during the early life history of estuarine fauna, particularly teleost fishes (Lenihan et al. 2001; Peterson et al. 2003; Stunz et al. 2010; zu Ermgassen et al. 2016). However, individuals may undergo ontogenetic shifts, expanding their movements to include a suite of habitats, presumably in response to size-specific shifts in resource requirements and risk of predation (Pittman et al. 2004; Bowler and Benton 2005). Effective implementation of restored oyster reef habitat requires an improved understanding of the relative importance of oyster reefs to adult fishes potentially using multiple habitats.

Spotted seatrout (*Cynoscion nebulosus*) is an estuarine-dependent species occurring from the Gulf of Mexico (GoM) to the northwest Atlantic (Bortone 2003). Previous studies have

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primarily used catch data to examine spotted seatrout habitat associations across the GoM. Seagrass beds, mud-sand substrate, and oyster reef have been identified as commonly used habitats, with dynamic variables such as temperature and salinity also shaping the distribution of spotted seatrout across estuarine habitats (Kupschus 2003; MacRae and Cowan Jr 2010; Froeschke and Froeschke 2011; Bramer 2015). Recent studies of spotted seatrout using acoustic telemetry have also identified sex-specific movements, spawning site fidelity, and interspecific habitat partitioning among estuarine habitats (Callihan et al. 2013; Lowerre-Barbieri et al. 2013; Moulton et al. 2017), but despite their high priority in restoration efforts, the relative importance of oyster reefs to spotted seatrout remains unclear.

A combined approach using natural tracers and electronic tagging can provide critical insights into behaviors and ecosystem-level interactions otherwise unobservable through the use of a single technique (e.g., Cunjak et al. 2005; Freedman et al. 2017; Muller and Strydom 2017). Dietary tracers such as stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) may reveal sources of organic matter and trophic position of an organism, respectively (Peterson and Fry 1987), integrating trends on temporal scales ranging from weeks to months, depending on the isotope turnover rate of the tissue type examined (Boecklen et al. 2011; Mohan et al. 2016). Muscle tissue is often used in studies examining trophic dynamics of fish, but sampling of muscle samples is often lethal. Alternative tissues, such as scales, have demonstrated utility as non-lethal dietary indicators in several species of teleost fishes (Hutchinson and Trueman 2006; Seeley and Walther 2017), including sciaenids (B. Walther, unpublished data). Linking habitat-specific movements with individual trophic dynamics may afford a more complete understanding of the functional role of specific habitats to spotted seatrout. Connecting individual variation in fish movement with resource use may improve our mechanistic understanding of the importance of oyster reef habitat to mobile sport fish.

In this study, we use a combination of acoustic telemetry techniques and the non-lethal sampling of natural dietary tracers ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), from the scales of tagged fish, to answer the following questions: (1) What are the temporal patterns of residency and fine-scale space use of spotted seatrout on restored oyster reef, and are these patterns related to fish size?; (2) How are patterns in space use influenced by environmental variables?; and (3) Does spotted seatrout trophic level or niche area differ with respect to fish size or residency?

Methods

Study Site

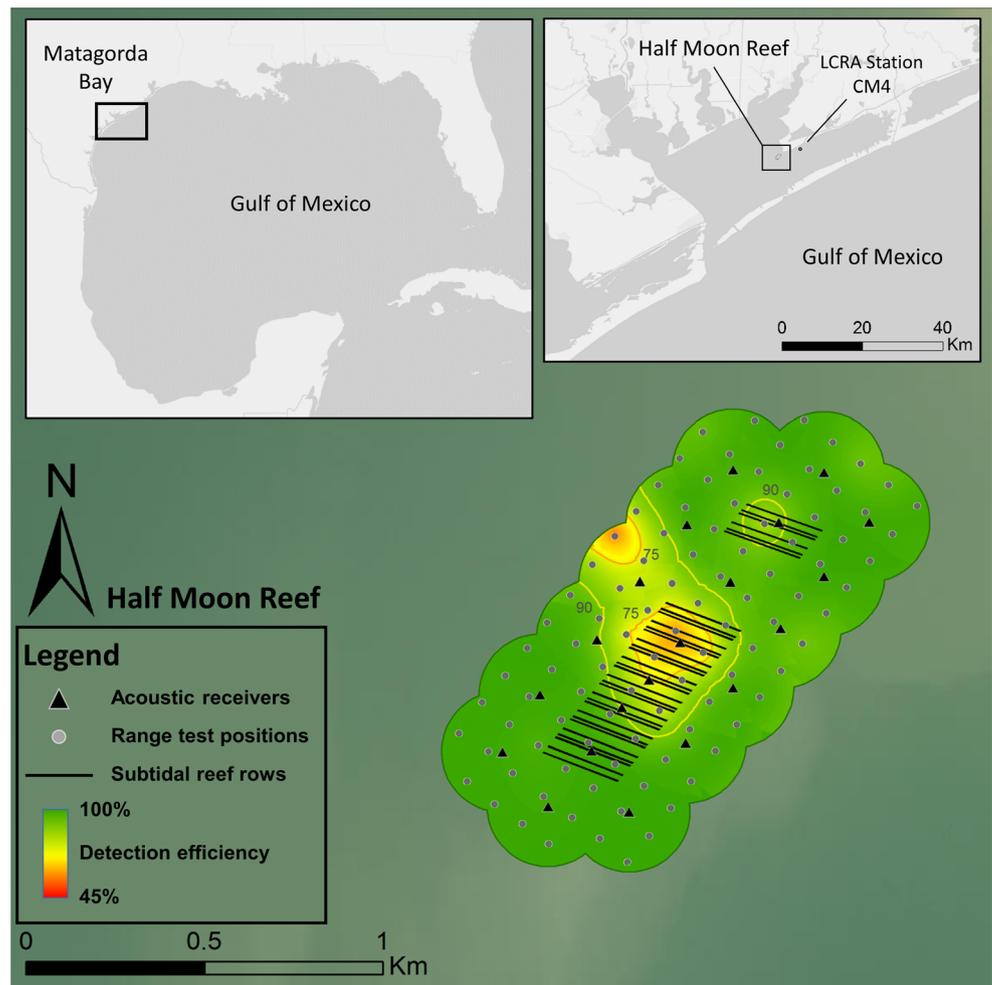
Half Moon Reef (HMR) is a 0.22-km² restored subtidal oyster reef complex constructed by The Nature Conservancy and the

US Army Corps of Engineers in 2014. HMR is located in central Matagorda Bay, Texas in water depths about 2 m deep. The reef rises within ~0.5 m of the surface at low tide, and is broken into two sections separated by ~250 m. These sections comprise a total of 32 parallel rows of limestone and concrete rubble heavily colonized by mature oysters (*Crassostrea virginica*), with rows within each section separated by a distance of ~15 m (Fig. 1). HMR experiences high levels of fishing pressure from both private and charter recreational anglers primarily targeting sport fish such as southern flounder (*Paralichthys lethostigma*), red drum (*Sciaenops ocellatus*), and spotted seatrout (Carlton et al. 2016).

Acoustic Array

Twenty passive acoustic receivers (Vemco VR2W) were deployed across HMR at ~150 m intervals (Fig. 1) from 10 December 2015 to 18 August 2016. Acoustic transmitters were programmed to emit a coded pulse train at random intervals every 100–180 s. When within detection range of an acoustic receiver, tag transmissions were logged by that receiver with a time/date stamp and the unique ID number for each fish. Receivers were mounted with the hydrophone oriented downward ~1 m from the surface on PVC pipes (13 mm diameter) driven into the substrate. Receivers were retrieved, downloaded and cleaned of biofouling every 3–4 months. Spatial and temporal variation in the effective detection range of receivers within the array was quantified via two range testing procedures. Temporal variation in detection efficiency of the array was quantified via permanent deployment of two transmitters (V9-1L, Vemco) on receiver moorings within the array (one on-reef, and one off-reef receiver). Stationary transmitters provided in situ estimates of expected hourly detection probabilities, which were used to correct for decreases in hourly detection probabilities occurring as a result of background noise interfering with transmitter signals (e.g., nocturnally soniferous fishes, alpheid shrimps), following Payne et al. (2010). Spatial variation in detection efficiency across the array was evaluated by calculating the proportion of successful detections of a test transmitter deployed ~0.5 m from the substrate at 99 locations (regularly spaced at 150 m intervals) across the array for a period of 3–4 min at each location. Detection efficiencies calculated at each location were then interpolated across the study site in ArcGIS (version 10.4, ESRI, Redlands, CA) to create a heat map of detection probability across the study site, and identify potential acoustic “shadows” in the array (Fig. 1). The average 50% detection range (range at which 50% of transmitter signals are detected by a receiver) was calculated from a logistic regression of detection successes and failures at varying distances ($n = 1980$; calculated as the distance from each range test location to each receiver).

Fig. 1 Map of study site at Half Moon Reef (HMR), Matagorda Bay, Texas, and placement of acoustic receivers (black triangles). Buffers surrounding receivers represent 50% detection range (183 m), and estimated spatial variation in detection probability across the array. Yellow and red lines represent estimated 90 and 75% detection efficiency isopleths, respectively. Location of Lower Colorado River Authority (LCRA) data logger CM4 shown in top right inset panel



Tagging

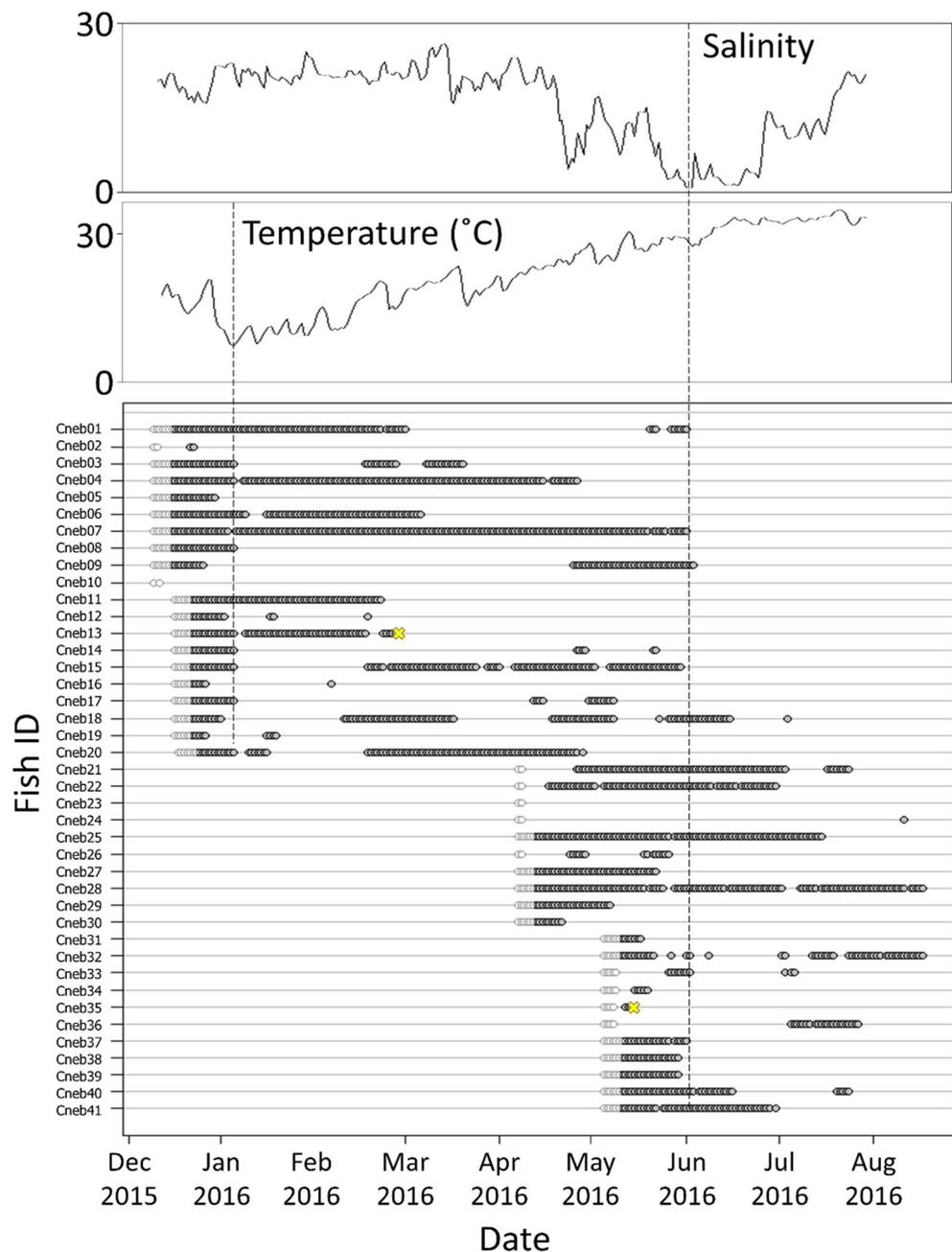
Spotted seatrout ($N=41$) were collected at HMR by hook-and-line baited with live shrimp or artificial lures. Upon capture, fish were measured, and those ≥ 375 mm total length (TL) (minimum legal size 380 mm TL) were selected for implantation of acoustic transmitters (V9-2H, Vemco). Transmitters were coated with a 3:2 paraffin-beeswax mix to prevent immune rejection (Lowe et al. 2003). Fish were anesthetized in a bath of tricaine methanesulfonate (MS-222, 100–150 mg l⁻¹) and a 1 cm incision was made lateral to the ventral midline with a sterile surgical scalpel. The tag was inserted into the peritoneal cavity, and the incision was closed using 1–2 interrupted absorbable sutures (Ethicon Chromic-Gut, Johnson & Johnson). For each fish, 2–6 scales were removed lateral to the dorsal fin and a T-bar anchor tag (Floy Tag & Mfg., Inc.) containing study contact information was inserted to identify tagged fish in case of recapture. Surgery times ranged from about 3–5 min. Upon completion of transmitter implantation and external tagging, fish were transferred to a holding tank containing seawater supplemented with oxygen.

Survival of tagged spotted seatrout using these techniques was expected to be high, based on previous experimental work on spotted seatrout surgical methods (Robillard et al. 2015).

Stable Isotope Analysis

About 2–6 scales were collected from tagged spotted seatrout ($N=41$). Scale and epaxial tissue were collected from additional spotted seatrout ($n=8$) not included in tagging study in order to validate the relationship between scale and muscle tissue stable isotope values. Scales collected from spotted seatrout were examined under a dissecting microscope to remove those showing signs of regeneration (a potential source of bias in scale isotope values). Scales selected for analysis were cleaned in ethanol, sonicated 5 min in Ultrapure water and air dried in plastic vials. Epaxial muscle tissue was rinsed in deionized water, dried in an oven and ground to a fine powder using ceramic mortar and pestle. About 1.6 mg of scale material (2–3 scales) and 1 mg dried muscle tissue was weighed on a microbalance, wrapped in tin capsules, and shipped to the University of California, Davis Stable Isotope

Fig. 2 Top panels: salinity and temperature records from Lower Colorado River Authority CM4 station, Matagorda Bay, Texas, during acoustic monitoring at HMR. Vertical dotted lines correspond to lowest observed temperature and salinity values during the study. Lower panel: abacus plot showing daily detections (gray circles) and angler recaptures (yellow crosses) of spotted seatrout at Half Moon Reef (HMR), Matagorda Bay, Texas. First 7 days of monitoring data for each individual excluded from analysis indicated by light gray circles



Facility for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis. A PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer was used for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis. Duplicates were included every 12th sample to assess precision. Mean difference between duplicate samples ($n = 5$) was 0.04‰ for $\delta^{13}\text{C}$ and 0.05‰ for $\delta^{15}\text{N}$.

Data Analysis

Patterns in spatial use within the study site and periods of presence/absence were identified through examination of time series of detection data. A detection was considered valid if a

fish was detected within the array at least twice in a 4-h period. Residence to the reef was estimated as a residency index, calculated as the percentage of days a fish was present on the reef relative to the total number of days at liberty (Cooke and McKinley 1999). Days at liberty were calculated as the number of days elapsed between tagging and the final date of the study. During the study, two fish were recaptured by recreational anglers (Table 1), and days at liberty for these fish were calculated as the number of days elapsed between tagging and recapture. Additionally, the frequency and duration of consecutive periods of presence or absence (forays) were calculated for each fish. To reduce potential confounding

Table 1 Summary data for spotted seatrout tagged at Half Moon Reef, Matagorda Bay, Texas. Residency index is the proportion of days at liberty in which a fish was detected, excluding first 7 days of data to minimize influence of tagging effects. Residency metrics excluded for fish not detected beyond 7 days after tagging. IDs shown in italics represent angler recaptures

| ID | Date tagged | Mass (g) | SL (mm) | TL (mm) | Days detected | Days at Liberty | Residency Index (%) |
|---------------|--------------------|------------|------------|------------|---------------|-----------------|---------------------|
| Cneb01 | 10 Dec 2015 | 510 | 350 | 403 | 83 | 244 | 34.0 |
| Cneb02 | 10 Dec 2015 | 575 | 345 | 403 | – | – | – |
| Cneb03 | 10 Dec 2015 | 775 | 370 | 435 | 43 | 244 | 17.6 |
| Cneb04 | 10 Dec 2015 | 765 | 397 | 450 | 127 | 244 | 52.0 |
| Cneb05 | 10 Dec 2015 | 445 | 330 | 386 | 13 | 244 | 5.3 |
| Cneb06 | 10 Dec 2015 | 495 | 330 | 386 | 74 | 244 | 30.3 |
| Cneb07 | 10 Dec 2015 | 560 | 350 | 405 | 163 | 244 | 66.8 |
| Cneb08 | 10 Dec 2015 | 520 | 336 | 390 | 19 | 244 | 7.8 |
| Cneb09 | 10 Dec 2015 | 665 | 380 | 420 | 49 | 244 | 20.0 |
| Cneb10 | 10 Dec 2015 | 1030 | 415 | 494 | – | – | – |
| Cneb11 | 17 Dec 2015 | 445 | 321 | 378 | 60 | 237 | 25.3 |
| Cneb12 | 17 Dec 2015 | 500 | 335 | 390 | 12 | 237 | 5.0 |
| <i>Cneb13</i> | <i>17 Dec 2015</i> | – | <i>360</i> | <i>412</i> | <i>57</i> | <i>237</i> | <i>24.0</i> |
| Cneb14 | 17 Dec 2015 | – | 325 | 380 | 18 | 237 | 7.6 |
| Cneb15 | 17 Dec 2015 | – | 340 | 395 | 103 | 237 | 43.5 |
| Cneb16 | 17 Dec 2015 | – | 351 | 405 | 4 | 237 | 1.7 |
| Cneb17 | 17 Dec 2015 | 545 | 343 | 395 | 25 | 237 | 10.6 |
| Cneb18 | 17 Dec 2015 | 535 | 347 | 405 | 89 | 237 | 37.6 |
| Cneb19 | 17 Dec 2015 | 580 | 345 | 400 | 7 | 237 | 2.9 |
| Cneb20 | 18 Dec 2015 | 680 | 375 | 433 | 88 | 237 | 37.1 |
| Cneb21 | 7 Apr 2016 | – | 365 | 418 | 77 | 125 | 61.6 |
| Cneb22 | 7 Apr 2016 | – | 347 | 419 | 71 | 125 | 56.8 |
| Cneb23 | 7 Apr 2016 | – | 375 | 446 | – | – | – |
| Cneb24 | 7 Apr 2016 | – | 336 | 403 | 1 | 125 | 0.8 |
| Cneb25 | 7 Apr 2016 | – | 361 | 425 | 91 | 125 | 72.8 |
| Cneb26 | 7 Apr 2016 | – | 365 | 429 | 14 | 125 | 11.20 |
| Cneb27 | 7 Apr 2016 | – | 331 | 394 | 38 | 125 | 30.40 |
| Cneb28 | 7 Apr 2016 | – | 391 | 465 | 113 | 125 | 90.40 |
| Cneb29 | 7 Apr 2016 | – | 332 | 387 | 23 | 125 | 18.40 |
| Cneb30 | 7 Apr 2016 | – | 328 | 386 | 7 | 125 | 5.60 |
| Cneb31 | 6 May 2016 | 595 | 339 | 401 | 5 | 103 | 4.85 |
| Cneb32 | 6 May 2016 | 685 | 350 | 418 | 47 | 103 | 45.63 |
| Cneb33 | 6 May 2016 | 660 | 331 | 403 | 11 | 103 | 10.68 |
| Cneb34 | 6 May 2016 | 630 | 336 | 395 | 5 | 103 | 4.85 |
| <i>Cneb35</i> | <i>6 May 2016</i> | <i>645</i> | <i>344</i> | <i>409</i> | <i>2</i> | <i>103</i> | <i>1.94</i> |
| Cneb36 | 6 May 2016 | 750 | 365 | 435 | 22 | 103 | 21.36 |
| Cneb37 | 6 May 2016 | 470 | 313 | 380 | 19 | 103 | 18.45 |
| Cneb38 | 6 May 2016 | 705 | 346 | 418 | 17 | 103 | 16.50 |
| Cneb39 | 6 May 2016 | 501 | 315 | 375 | 17 | 103 | 16.50 |
| Cneb40 | 6 May 2016 | 615 | 333 | 395 | 39 | 103 | 37.86 |
| Cneb41 | 6 May 2016 | 525 | 320 | 384 | 53 | 103 | 51.46 |

effects of capture/handling or tag implantation on fish behavior, the first 7 days of detection data were excluded from all subsequent analyses. All subsequent analyses of residency were performed for a subset of seatrout ($n = 38$), as three fish did not remain on the reef for a period longer than 7 days following capture and tagging (Table 1). Spectral (Fast

Fourier Transformed) analysis of hourly detections pooled across all tagged fish was performed to identify dominant cyclical periods in detection counts that might indicate cyclical patterns of activity at HMR (e.g., diel or tidally associated movements). Fine-scale space use on HMR was evaluated through the use of center of activity (COA) analysis. A mean

position (short-term COA) was calculated every 30 min for each fish from the mean location (latitude, longitude) of receivers on which a fish was detected, weighted by the number of detections at each receiver (Simpfendorfer et al. 2002). To provide estimates of long-term core use areas of HMR, Kernel Density Estimates (50%, 75% KDEs) based on COA were calculated using the *rhR* library (Signer and Balkenhol 2015) in R (version 3.3.1, R Development Core Team 2016) and plotted in ArcGIS (version 10.4, ESRI, Redlands, CA). Areas constrained by a 50% KDE isopleth represent areas of core use, and the smallest possible polygon containing 50% of fish locations (i.e., the smallest area having a 50% probability of containing a specific tagged individual).

Hourly temperature ($^{\circ}\text{C}$), salinity, and tide height (m, relative to mean lower low water, MLLW) data were obtained (<http://waterquality.lcra.org>) at station CM4 (28.58174 $^{\circ}$, -96.18799 $^{\circ}$), with a data sonde moored at a fixed depth of ~ 1 m from the bottom, about 5 km east of the study site. Generalized additive models (GAMs) were used to examine the relationship between environmental variables and the presence-absence of spotted seatrout on HMR. Models were fit using a binomial distribution and logit link in the *mgcv* library (Wood 2006) in R, with individual fish included as a random factor. Temperature, salinity and tide height were included as environmental predictors and constrained to three degrees of freedom to avoid model overfitting. Stepwise backward variable selection was used to select the best model of spotted seatrout presence-absence, where variables were sequentially removed with the goal of minimizing Akaike information criterion (AIC) values. If removal of a variable resulted in a $\Delta\text{AIC} < 2$ when models were compared, the variable was retained in the final model (Burnham and Anderson 2002).

To validate the use of scale tissue as a non-lethal alternative to epaxial muscle tissue as a dietary tracer for tagged fish, the relationship between stable isotope values obtained from paired scale and muscle tissue collections was evaluated via linear regression. Mean tissue discrimination factors (i.e., the mean difference between isotope values from each tissue; $\delta_{\text{muscle}} - \delta_{\text{scale}}$) were calculated for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Ontogenetic shifts in trophic ecology were examined through linear regressions of scale $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ against TL. The SIBER library (Jackson et al. 2011) in R was used to estimate Bayesian standard ellipse areas (SEA_{B}), expressed in units of per mil squared ($\% \sigma^2$), for fish showing high ($> 50\%$) and low ($< 50\%$) residency to HMR. To test the hypothesis that spotted seatrout with increased residence to HMR occupy a narrower isotopic niche, posterior estimates of SEA_{B} for high residency and low residency spotted seatrout were used to calculate $P(\text{SEA}_{\text{B, High Residency}} > \text{SEA}_{\text{B, Low Residency}})$ with values < 0.05 indicating significant differences in isotopic niche area.

Results

Range Testing

Detection efficiency across the study site was high (Fig. 1), with relatively low spatial variability ($93 \pm 16\%$; mean \pm SD). Detection efficiency was poorest in areas of high relief towards the northern extent of the south reef segment. Consistently high detection efficiency in the majority of areas across the study site suggest extended periods of absence (hours–days) for tagged fish are unlikely to be an artifact of fish moving into areas of the reef not effectively monitored by acoustic receivers. Logistic regression of detection efficiencies at each of 99 range test locations indicated a 50% detection range of 183 m.

Space Use

A total of 41 spotted seatrout ranging from 352 to 494 mm TL were tagged at HMR between 10 December 2015 and 6 May 2016 (Fig. 2) and monitored through 18 August 2016. Days at liberty for individual fish ranged from 103 to 244 days (mean 174 days). Two tagged fish (Cneb13, Cneb35) were recaptured by recreational anglers during the study; Cneb13 was recaptured after 72 days within the HMR array, while Cneb35 was recaptured about 7 km southeast of HMR, 31 days after tagging. Overall, spotted seatrout exhibited low residency to HMR ($17 \pm 22\%$ of days present; median \pm S.D.), though there was considerable variation in patterns of presence across the study period and among individuals. When broken into periods of consecutive presence or absence (forays), fish were present for intervals of 56 ± 36 days (median \pm S.D.) and absent for intervals of 15 ± 21 days. Though no trends were apparent in the number or frequency of forays away from HMR, there was a significant positive relationship ($F_{(1,35)} = 11.22$, $r^2 = 0.22$, $p = 0.002$) between spotted seatrout TL and residency to HMR (Fig. 3). Spotted seatrout movements at HMR were concentrated towards the inner portions of the reef and the sand/mud channel adjoining north and south reef sections, with limited use of the sand/mud flats surrounding the reef (Fig. 4). Individual seatrout used relatively small core use areas ($0.105 \pm 0.030 \text{ km}^2$; median \pm S.D.) at HMR (Fig. 5). Core use areas followed 4 general distribution patterns across HMR: (1) Central HMR, (2) South HMR, (3) North HMR, and (4) bimodal use of South and North HMR (Fig. 6). Spectral analysis of pooled hourly detection counts over the course of the study revealed strong cyclical patterns in detections on the reef occurring at 12 and 24 h intervals (Fig. 7).

Environmental Factors

Two instances of highly synchronized short-term (< 30 days) migrations away from HMR were observed on 5 January

Fig. 3 Linear regression of total length and residency (percentage of days present) of spotted seatrout at Half Moon Reef, Matagorda Bay, Texas

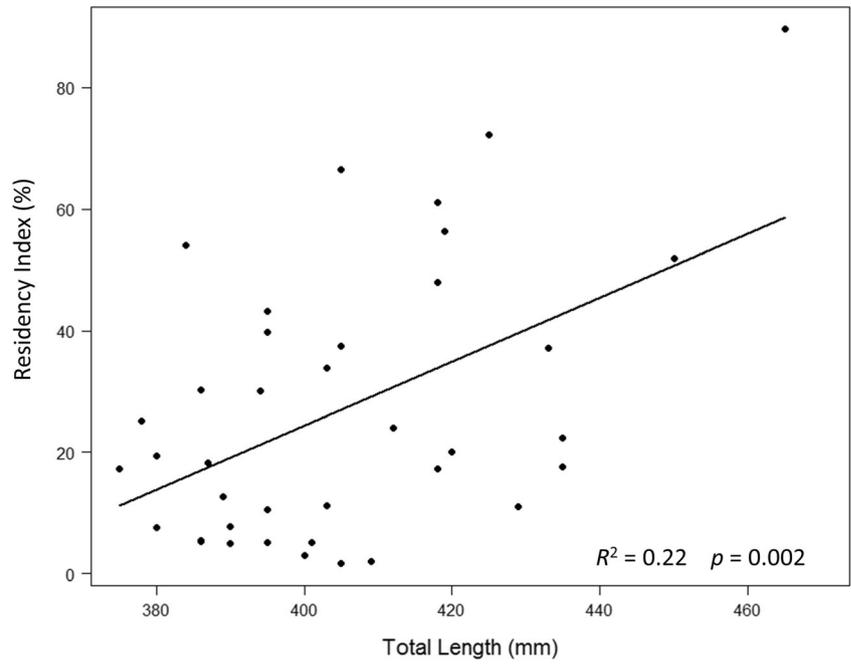
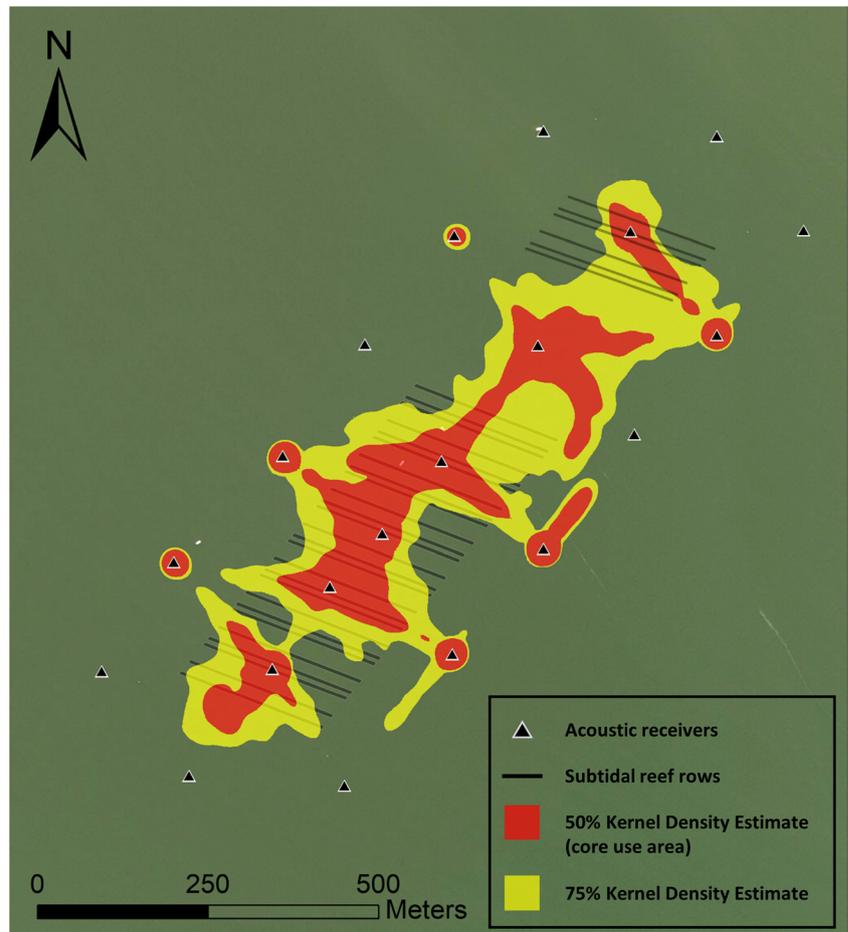


Fig. 4 Kernel Density Estimates (50%, 75%) of spotted seatrout at Half Moon Reef, Matagorda Bay, Texas. Black triangles represent acoustic receiver locations, black lines indicate rows of limestone cobble/restored oyster reef



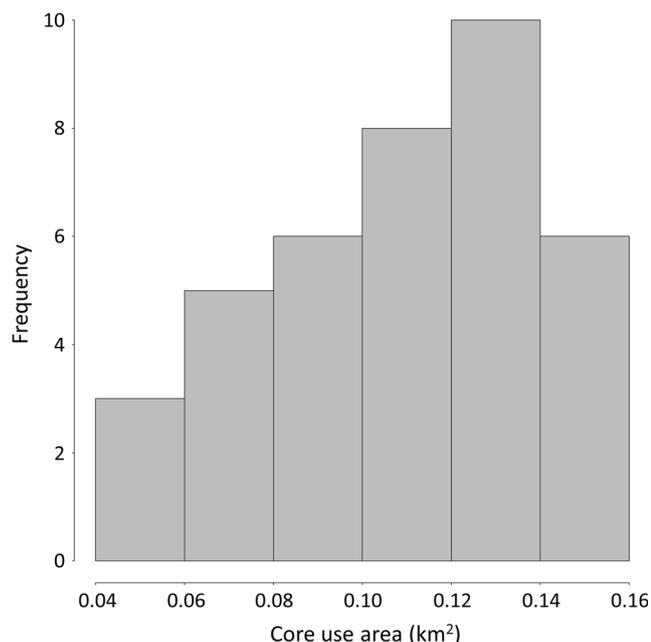


Fig. 5 Histogram of individual core use areas (50% kernel density estimates) of spotted seatrout at Half Moon Reef, Matagorda Bay, TX

(50% of tagged fish) and 3 June 2016 (55% of tagged fish). The timing of each of these emigration events was accompanied, respectively, by the lowest water temperature (10.1 °C) and salinity (0.33) values recorded over the course of the study (Fig. 2). Environmental factors (temperature, salinity, tide height) each had a significant influence ($p < 0.001$) on hourly presence-absence of spotted seatrout at HMR (Fig. 8). The best-fit model explained 18.9% of the total deviance, and retained temperature, salinity, and tide height. Temperature had the greatest influence on spotted seatrout presence at HMR ($\Delta\text{AIC} = 773$). The greatest presence of tagged individuals was predicted at moderate temperatures (15–25 °C; $\Delta\text{AIC}: 217$), low salinities (5–10; $\Delta\text{AIC}: 203$), and at positive tide heights (> mean lower low water; $\Delta\text{AIC} = 203$).

Stable Isotope Analysis

Stable isotope values obtained from scales were strongly correlated with muscle stable isotope values ($\delta^{13}\text{C}$: $F_{(1,6)} = 25.63$, $r^2 = 0.78$; $p = 0.002$, $\delta^{15}\text{N}$: $F_{(1,6)} = 25.02$, $r^2 = 0.81$; $p = 0.002$):

$$\delta^{13}\text{C}_{\text{muscle}} = 0.371(\delta^{13}\text{C}_{\text{scale}}) + 11.176$$

$$\delta^{15}\text{N}_{\text{muscle}} = 0.633(\delta^{15}\text{N}_{\text{scale}}) - 9.769$$

Mean tissue discrimination factors were 3.9 ± 0.5 (\pm SD) for $\delta^{13}\text{C}$ and 0.6 ± 0.6 for $\delta^{15}\text{N}$. Values for $\delta^{13}\text{C}$ from spotted seatrout scale tissue at HMR ranged from -18.20 to -13.04‰ (-16.06 ± 1.04 ; mean \pm SD), while $\delta^{15}\text{N}$ ranged from 14.84 to 17.73‰ (16.63 ± 0.75 ; mean \pm SD)(Fig. 9a). No significant relationship was observed between fish size

(TL) and $\delta^{13}\text{C}$ ($p = 0.22$) or $\delta^{15}\text{N}$ ($p = 0.10$), though $\delta^{15}\text{N}$ increased slightly with TL. Fish exhibiting high residence ($n = 8$) occupied significantly smaller isotopic niches (mode: 0.79‰^2 , 95% credible interval: $0.34\text{--}1.68\text{‰}^2$) than low residence fish ($n = 30$, mode: 2.38‰^2 , 95% credible interval: $1.66\text{--}3.56\text{‰}^2$, $P(\text{SEA}_{\text{B, High Residence}} > \text{SEA}_{\text{B, Low Residence}}) = 0.011$) (Fig. 9b).

Discussion

Spotted seatrout exhibited continued use of oyster reef habitat at HMR over the course of the study period, though there was considerable variation in residency among individuals, with fish spending 1–90% (mean \pm SD: $23.8 \pm 22.3\%$) of monitoring days within the array. In a similar study of spotted seatrout in Texas estuarine habitats, Moulton et al. (2017) reported greater overall residency ($\sim 58\%$ of monitoring days) to a study site containing multiple habitat types, though fine-scale analysis identified preferential use of seagrass and mud-sand habitats relative to oyster reef. HMR is situated in deeper water (~ 2 m), and is characterized by greater vertical relief, than many natural oyster reefs throughout the Gulf Coast, which may increase the accessibility or utility of this habitat in comparison to intertidal oyster reefs elsewhere. It is also unknown whether the age of HMR in comparison to older natural reefs influenced patterns of use by spotted seatrout. Some of the individual variability in residency of fish in our study was explained by fish total length (TL), where residency to HMR increased linearly with TL (> 50% residency predicted for fish > 450 mm TL). Spotted seatrout tagged at HMR were larger (range 352–494 mm TL) than those in Moulton et al. (2017)(240–308 mm TL). If smaller (< 450 mm TL) spotted seatrout indeed exploit a wider range of habitats than larger (> 450 mm TL) individuals, this may in part explain the increased residency of fish to an array containing multiple habitats, as well as the apparent increased use of oyster reef habitat by larger fish at HMR relative to Moulton et al. (2017). Size-related differences in residency observed in fish tagged at HMR are likely related to shifts in foraging behavior with increasing size. It is possible that oyster reef serves as a secondary habitat for smaller (< 450 mm TL) fish primarily foraging elsewhere, in contrast to larger (> 450 mm TL) spotted seatrout, which might base their movements from the oyster reef habitat of HMR. However, there was no clear association between number of forays, average consecutive days present (or absent), and fish size at HMR.

Spotted seatrout are batch spawners with indeterminate fecundity that spawn throughout a protracted spawning season (Brown-Peterson 2003), and spawning frequency increases with body size (Cooper et al. 2013). While seatrout presence-absence at HMR may have been influenced by spatiotemporal spawning patterns, due to the relatively short

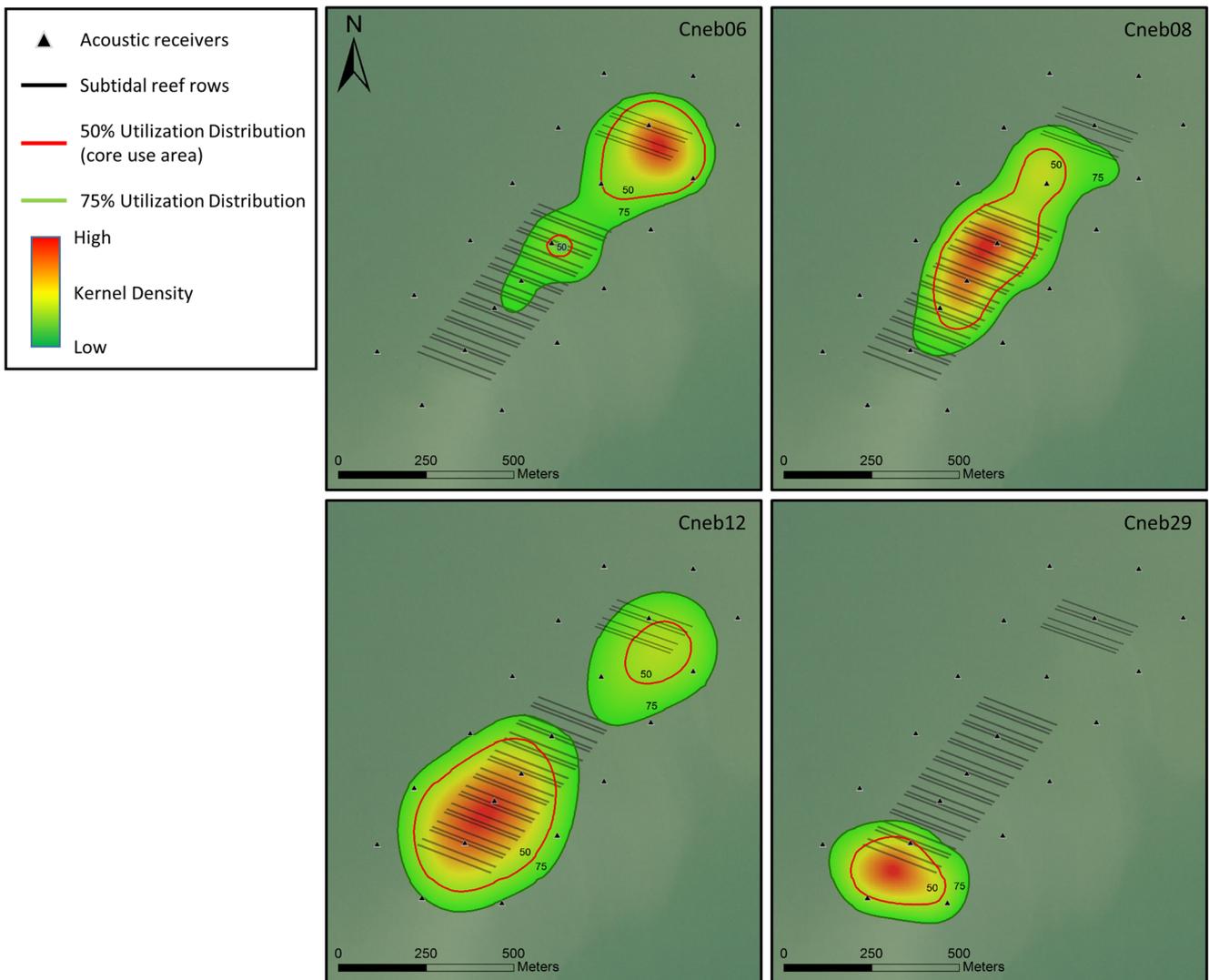
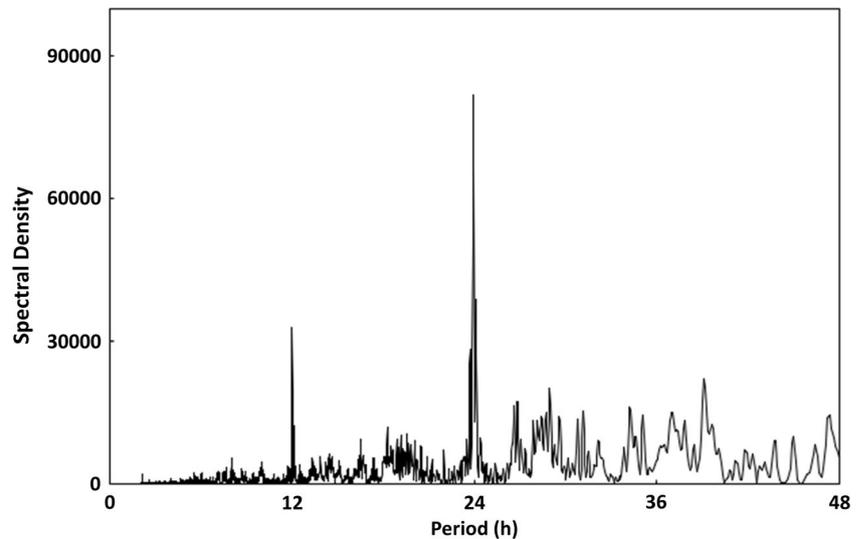


Fig. 6 Space use of individual spotted seatrout (Cneb06, Cneb08, Cneb12, Cneb29) at Half Moon Reef, Matagorda Bay, Texas, exemplifying four main patterns of distribution across the study site. Black triangles represent acoustic receiver locations, black lines indicate

rows of limestone cobble/restored oyster reef. Red and green contour lines represent 50% (core use area) and 75% kernel density estimates. Color ramp represents density of kernel density estimates increasing from green to red

Fig. 7 Spectral analysis of Fast Fourier Transformed (FFT) hourly detections of spotted seatrout at Half Moon Reef, Matagorda Bay, Texas. Peaks in spectral density (y-axis) represent temporal periodicity of detections



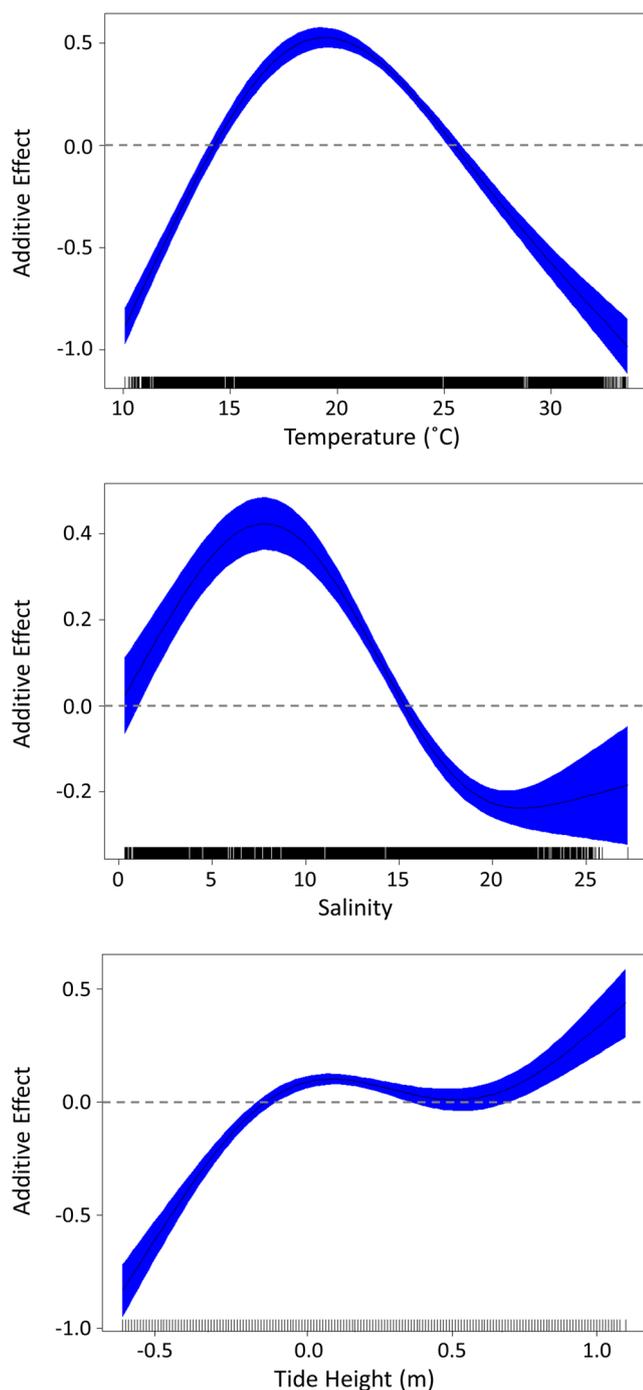


Fig. 8 Response plots from generalized additive mixed model showing relationship between environmental predictors (temperature, salinity, tidal height) and hourly presence-absence of spotted seatrout at Half Moon Reef, Matagorda Bay, Texas

monitoring period and staggered tagging of spotted seatrout at HMR, we were unable to address spawning related or seasonal movements in this study. Sex-specific differences in the emigration timing of adult spotted seatrout were described in Callihan et al. (2013), and though we did not determine fish sex in this study, it is possible that the variation in residency

among individuals could also be explained by sex. Spotted seatrout used the majority of available oyster reef habitat at HMR, showing limited use of soft bottom habitats, with the exception of a broad sand/mud channel separating the north and south reef sections. It is not clear why spotted seatrout exhibited increased use of the soft bottom channel located between the northern and southern sections of HMR, but spotted seatrout may have been exploiting oyster/soft bottom ecotone for foraging purposes. Though spotted seatrout tagged in this study were relatively large (375–494 mm TL), the increased vertical relief provided by HMR may also serve as refuge from spotted seatrout predators found throughout the region (e.g., bull shark (*Carcharhinus leucas*), bottlenose dolphin (*Tursiops truncatus*); TinHan et al. unpublished, Barros and Odell 1995). Individual fish exhibited relatively high fine-scale residency to specific portions of the reef. It is somewhat surprising that the movements of individual fish did not expand to include more of the available reef habitat at HMR. Due to the uniform distribution, depth and arrangement of oyster reef habitat at HMR, as well as the distribution of core use areas across the majority of the reef area, it seems unlikely that differences in space use among individuals are driven by fine-scale differences in habitat suitability within HMR.

Linking stable isotope data to movement patterns determined with telemetry assumes consistent patterns of behavior before and after tagging, since stable isotope values only reflect fish diet prior to tagging and tissue collection. Strong relationships in values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between scale and muscle tissue have been reported in other teleost fishes (Perga and Gerdeaux 2003; Kelly et al. 2006). However, due to scale growth patterns (i.e., under plating), stable isotopes obtained from scale tissue are reflective of more recent trophic history due to scale architecture (Hutchinson and Trueman 2006). In spotted seatrout from HMR, scale isotope values were significantly related to muscle tissue values, suggesting isotope turnover rates on the order of 30–60 days for 50% equilibration to distinct diets, or > 100 days for 95% equilibration to diet, for studies that have estimated muscle tissue turnover in sub-adult fish (Suzuki et al. 2005; Buchheister and Latour 2010; Mohan et al. 2016). Thus, isotope values obtained from spotted seatrout scales likely integrate trophic histories over a 3–4-month period leading up to the time of capture. Quevedo et al. (2009) identified intrapopulation decreases in trophic niche breadth in Eurasian perch (*Perca fluviatilis*) primarily using less diverse pelagic habitat, in contrast to conspecifics using more complex littoral habitats, and exhibiting greater trophic niche breadth. Here we observed a similar relationship between habitat use and trophic niche breadth, where spotted seatrout exhibiting greater residency to HMR also occupied significantly smaller isotopic niches. This may suggest that fish with decreased residency to HMR (< 50%) rely upon a wider range of prey items across multiple habitats and food webs than resident fish primarily occupying oyster reef food webs. However, our sample

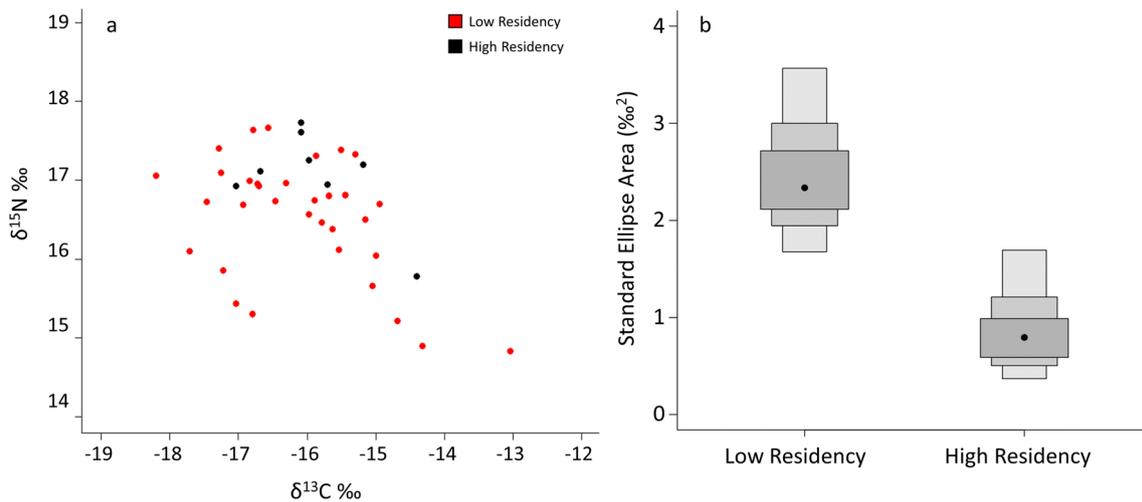


Fig. 9 **a** Biplot of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ values for scale tissue from spotted seatrout at Half Moon Reef (HMR), Matagorda Bay, Texas, exhibiting high (> 50%; black filled circles) and low (< 50%; red filled circles) residency to HMR. **b** Boxplots representing distribution of Bayesian standard ellipse

areas (SEA_B) calculated for spotted seatrout exhibiting low and high residency to Half Moon Reef, Matagorda Bay, Texas. Shaded boxes represent, from dark to light gray, 50, 75, and 95% credible intervals. Black dots represent SEA_B modes

size for high residency fish ($n = 8$) was less than the minimum number of samples ($n = 10$) recommended for precise Bayesian ellipse area estimation (SEA_B ; Jackson et al. 2011), therefore these results should be interpreted with caution. Differences in trophic niche breadth may also be influenced by dietary and habitat shifts alike (Newsome et al. 2007; Flaherty and Ben-David 2010). However, the relatively narrow size range of adult fish tagged in this study, along with the lack of significant relationship between fish size $\delta^{15}\text{N}$ and fish size, precludes ontogenetic dietary shifts as important factors affecting trophic niche breadth.

Previous studies of habitat suitability in spotted seatrout in the GoM have identified temperature and salinity as primary drivers of occurrence. The majority of these studies have focused on early life stage fish, but it has been suggested that optimal conditions estimated for juvenile occurrence are consistent with those of adult fish (Baltz et al. 2003). Like many estuarine fishes, spotted seatrout are eurythermal and euryhaline, and studies estimating environmental preferences for this species typically report temperatures between 15 and 30 °C and salinities ranging from 10 to 20 (Kupschus 2003; Froeschke and Froeschke 2011). However, spotted seatrout exhibit a critical limit of cold tolerance between 3 and 4 °C (Ellis et al. 2017), with functional limitation of respiratory metabolism in salinities < 10 and > 45 (Wohlschlag and Wakeman 1978). Two instances of highly synchronized short-term (< 30 days) migrations away from HMR were observed on 5 January 2016 (50% of tagged fish) and 3 June 2016 (55% of tagged fish). Each of these emigration events corresponded, respectively, with the lowest water temperature (10.9 °C) and salinity (0.33) values observed at sonde station CM4 over the course of the study. Presence of spotted

seatrout at HMR was greatest during periods of moderate temperature (18–20 °C) and moderate-low salinity (7–10). One explanation for the disparity in preferred salinities observed at HMR relative to previous estimates may be that HMR affords advantages that offset the physiological challenges of remaining in suboptimal salinity or water temperature (e.g., refuge from predation, increased access to prey resources). The duration of unfavorable environmental conditions may also play a role; salinity declined below 5 for a period of 7 days, 1 month prior to the synchronized migration in early June, but this was not accompanied by any decrease in daily presence-absence of tagged fish at HMR. Alternatively, short periods of increased precipitation and runoff might have produced vertically or horizontally stratified conditions under which salinities or temperatures recorded at sonde station CM4 did not accurately reflect salinity conditions at HMR. Another possibility is that during periods of increased stratification, spotted seatrout may simply remain below unfavorable surface waters, rather than undertaking potentially risky and energetically demanding forays to more favorable conditions. However, such periods may be uncommon, given the shallow depths of HMR and wind driven mixing in the region (McCarthy and Gardner 2002).

In this study, we used a dual natural tracer and acoustic tagging approach to quantify the habitat use and trophic dynamics of spotted seatrout in relation to restored oyster reef habitat. While the overall residence of spotted seatrout to HMR was low, individual core use areas on the reef were relatively small (~50% of HMR). This indicates that, although spotted seatrout may regularly use other habitats over longer temporal scales (months–years), habitat patches such as oyster reef may not need to be very large to contain the

majority of spotted seatrout movements over shorter temporal scales (weeks–months). Short- and long-term patterns of presence-absence on the reef were strongly influenced by regional fluctuations in temperature, salinity and tidal height. However, the majority of spotted seatrout migrating away from the reef after seasonal lows of temperature and salinity returned and resumed use of the reef habitat shortly thereafter. Spotted seatrout residency at HMR increased with body size, highlighting the potential importance of this habitat to a recreationally important sport fish. The non-lethal sampling of scale tissue for stable isotope analysis revealed decreasing trophic niche breadth for larger individuals, suggesting greater reliance upon oyster reef food webs than smaller, less resident spotted seatrout. Due to the inherent difficulty of quantifying specific benefits of restored habitat for older age classes of fishes, efforts to quantify the enhancement of fish populations over these habitats have focused primarily on estimating recruitment enhancement. More recently, zu Ermgassen et al. (2016) incorporated estimates of the proportional use of oyster reef habitat by adult fishes into models of enhancement, underscoring the need for studies linking habitat use and trophic ecology. Intrapopulation differences in feeding ecology and habitat use may also play an important role in mediating the intensity of trophic connectivity among food webs and discrete habitats (Quevedo et al. 2009), and future studies aimed at identifying these relationships will improve our ability to predict the role of habitat restoration in ecosystem-based management approaches.

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