HABITAT USE AND CONNECTIVITY OF JUVENILE RED DRUM AND SPOTTED SEATROUT ACROSS ESTUARINE SEASCAPES

A Thesis

by

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ABSTRACT

Red drum (*Sciaenops ocellatus*) and spotted seatrout (*Cynoscion nebulosus*) are important gamefish that co-occur in estuarine seascapes throughout their range and support recreational fisheries of considerable economic value. Management of these species is compromised by knowledge gaps regarding habitat use and connectivity of late juveniles at multiple spatial scales. Thus, habitat-scale (~1 m to 1 km) and bay-scale (~1 to 50+ km) tracking was conducted using acoustic telemetry in an estuarine system on the coast of Texas, including a large portion of the Mission-Aransas National Estuarine Research Reserve (MANERR) and associated waters. Habitat-scale tracking was conducted for one month using an acoustic positioning system consisting of 20 acoustic receivers, which triangulated fish position with high spatial resolution. Bay-scale tracking occurred over a two year period and employed 45 acoustic receivers placed in several bays and two tidal passes.

Habitat-scale tracking revealed that seagrass was used extensively by each species, and red drum were also associated with oyster reef and boundaries between habitat types. Habitat partitioning was observed as spatial overlap between the two species was limited, with red drum commonly observed in shallower water depths than spotted seatrout. Diel shifts in habitat use and rate of movement were documented for each species and possibly linked to shifts in foraging activity. Bay-scale tracking primarily revealed restricted movement within bays, and final displacement of both species was typically less than 5 km. Directed bay-scale movement was greatest in winter and spring for both species, when a small contingent of individuals made directed movements of up to 70 km. Results of the study indicate that habitat use and movement were species-specific and subject to temporal variation, both diel and seasonal. Habitat-scale connectivity was influenced by seascape structure and water depth, and bay-scale connectivity was generally limited, suggesting that the sustainability of these fisheries is tied to local conditions.

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INTRODUCTION

Juveniles of many economically valuable fish species depend on estuaries for nursery habitat. Unfortunately, estuaries are particularly vulnerable to anthropogenic stressors (e.g. habitat loss), which can alter nursery function and negatively impact year-class strength (Kennish 2002). Studies comparing the value of specific nursery habitats or regions occupied during early life are needed to help prioritize conservation and restoration efforts, because resources supporting these efforts are often limited (Beck et al. 2001). Evaluating the relative value of habitats and/or nursery areas is often complicated by the complex arrangement of habitat types or patches within an estuarine seascape (Grober-Dunsmore et al. 2009). Habitat patches of varying size, shape, and water depth can be functionally connected as a part of larger mosaics and collectively serve a nursery function (Nagelkerken et al. 2014). In response, detailed assessments of habitat use and connectivity are needed to determine the relative value and functional role of habitat types or areas used during early life (Beck et al. 2001).

A variety of approaches have been used to assess habitat use and connectivity of estuarine fishes, and acoustic telemetry has become popular due to its improved spatial and temporal resolution over traditional techniques such as hard-part chemistry, mark-recapture, or fishery-independent sampling (Cunjak et al. 2005; Heupel 2006). Passive acoustic receivers can be deployed for long periods of time with little required maintenance to continuously monitor fish presence (Heupel 2006). Strategically placed receivers can provide information about habitat use, residency, and connectivity, and the timing of detections can yield information about both the direction and rate of movement. Traditionally, passive telemetry data has lacked the spatial resolution needed to determine fine-scale habitat use, indicating only presence within a receiver's detection range. However, high-density arrays of passive acoustic receivers with overlapping detection ranges, commonly referred to as acoustic positioning systems, provide researchers with a novel tool that can be used to triangulate an individual's position with high accuracy (~ 1-2 m, Espinoza et al. 2011a). Data from acoustic positioning systems have been combined with high-resolution maps to elucidate habitat use and connectivity of fishes within estuarine seascapes (Espinoza et al. 2011b; Farrugia et al. 2011; Furey et al. 2013).

Acoustic telemetry was used in the current study to examine habitat use and connectivity of two sympatric gamefishes, red drum (*Sciaenops ocellatus*) and spotted seatrout (*Cynoscion nebulosus*), within the Mission-Aransas National Estuarine Research Reserve (MANERR) and adjacent waters. Red drum and spotted seatrout are both estuarine dependent as juveniles, and newly settled individuals are commonly associated with submerged aquatic vegetation (i.e., seagrass) and salt marsh (Rooker et al.1998; Stunz et al. 2002). Although the early life history (larval to early juvenile stages) of red drum and spotted seatrout has been well-studied (e.g., Peters and McMichael 1987; McMichael and Peters 1989; Rooker and Holt 1997; Neahr et al. 2010), comparable information on late juveniles (defined here as age 1+) is very limited (Adams and Tremain 2000; MacRae and Cowan 2010). Previous research has shown that each species uses a wide variety of estuarine habitats during the late juvenile stage

(Bacheler et al. 2009; MacRae and Cowan 2010), and both species are capable of making broad (> 100 km) movements across bays and large seascapes (Arnoldi 1984; Bacheler et al. 2009; Payne 2011). Still, studies using natural tracers (otolith chemistry) indicate that ecologically relevant scales of connectivity for both red drum and spotted seatrout are likely less than 100 km (Comyns et al. 2008; Rooker et al. 2010), and therefore an improved understanding of habitat use and movement by both species is warranted.

Although recent research has improved understanding of the dispersive behaviors of both red drum and spotted seatrout, knowledge gaps regarding habitat use and connectivity still exist, compromising the development of effective management plans for the late juvenile stage. Therefore, the aim of the present study was to characterize habitat use and movement of both species within the MANERR at two spatial scales: habitat-scale (~1-1000 m) and bay-scale (~1-50+ km). In addition, this study also examined the influence of ontogeny (age-1 vs. age-2) and temporal factors (e.g. time of day, season) on the habitat use and movement of both species within the MANERR and associated waters.

METHODS

The study was conducted in an extensive estuarine bay system located on the central coast of Texas and protected from the Gulf of Mexico (GoM) by barrier islands (Figure 1). The majority of the northern area of the system is contained within the MANERR (Figure 1). Primary submerged habitats in the system include seagrasses and oyster reef. The most common seagrasses, shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*), are prevalent throughout the MANERR and associated waters, while oyster reef is mainly concentrated in Copano Bay, Carlos Bay, Mesquite Bay, and the northern region of Aransas Bay. The system receives variable but limited freshwater input, and hypersaline conditions may occur during periods of drought.

Two arrays of acoustic receivers (hereafter referred to as “habitat-scale” and “bay-scale” arrays) were deployed between May and July 2013 to assess habitat-scale and bay-scale habitat use and connectivity, respectively. The majority of the bay-scale array was deployed first, as 31 receivers (Vemco VR2W) were distributed in late May and early June 2013 across the system ranging from Corpus Christi Bay to Mesquite Bay to ensure that each bay was being monitored (Figure 1). Receivers were also positioned at the two primary tidal passes connecting the system to the GoM (Packery Channel and Aransas Pass), and near the mouths of the Mission River and Aransas River, both of which enter the greater Copano Bay area (Figure 1). Once the framework of the bay-scale array was in place, a habitat-scale array consisting of 20 acoustic receivers (Vemco VR2W) was deployed at Mud Island in Aransas Bay. Following the conclusion of

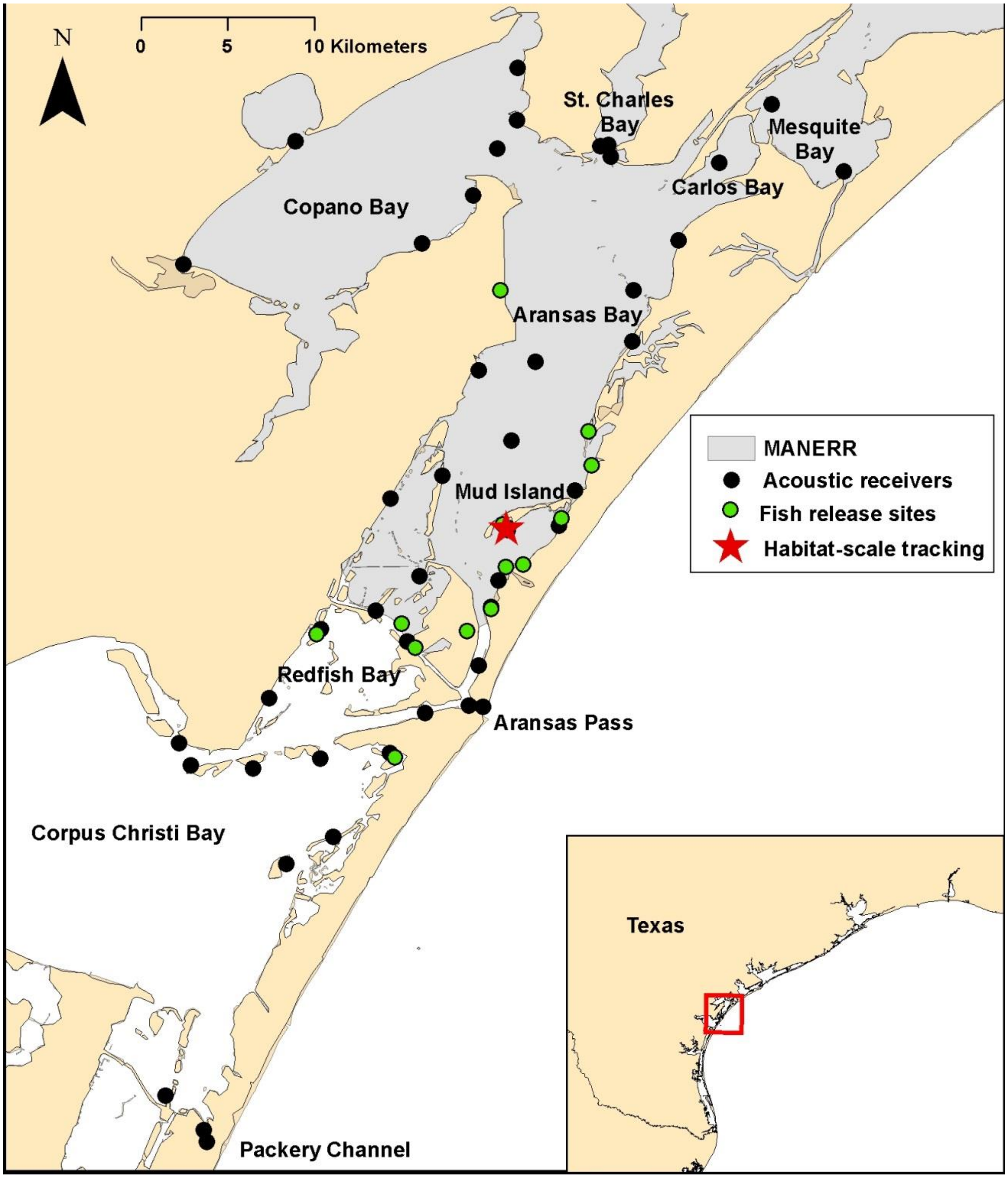

Figure 1. Map of Mission-Aransas National Estuarine Research Reserve (MANERR) and associated waters. Forty-five acoustic receivers were deployed for bay-scale monitoring of late juvenile red drum and spotted seatrout from June 2013 to May 2015. The red star represents the location of the habitat-scale tracking array at Mud Island.

habitat-scale tracking in early July, two receivers were left in place at Mud Island and 12 others were repositioned to enhance the spatial coverage of the bay-scale array, bringing the total number of receivers in the bay-scale array to 45 (Figure 1). Receivers deployed at channel markers or other available wooden posts were bolted to a galvanized pipe, and receivers in habitat areas lacking wooden structure (including the entire habitat-scale array) were cable-tied to polyvinyl chloride (PVC) pipe. The bay-scale array remained in place until May 2015, when expected transmitter life had expired. Receivers were serviced and downloaded biannually, and occasional losses occurred during the study such that 39 receivers remained at the conclusion.

Mud Island, the site of the habitat-scale array, is a complex of smooth cordgrass (*Spartina alterniflora*) and black mangroves (*Avicennia germinans*) that shelter a shallow inner lagoon from the open expanses of Aransas Bay. The array encompassed an area of 145,000 m^2, including a variety of habitat types and the bathymetry gradient from the open bay to the inner lagoon. Habitat types were classified using orthorectified satellite imagery verified by ground observation. Selected habitat boundaries as well as a grid of 661 points were examined in the field to record habitat type and water depth. Habitats included seagrass (mixed beds with overall proportion of 71% shoal grass *Halodule wrightii*, 25% turtle grass *Thalassia testudinum*, and 4% manatee grass *Syringodium filiforme*), oyster reef (live oyster and fringing shell), and mud or sand sediment including up to 15% seagrass coverage (hereafter collectively referred to as “bare” substrate). Recorded depths were corrected by tidal height following the method of Furey et al. 2013 and interpolated throughout the study site using universal kriging in the Spatial Analyst extension of ArcGIS 10.0 (ESRI, Redlands CA). Water depth in the inner lagoon was generally less than 1 m, even during the highest tides. Water depth increased gradually on the open bay side, where the array encompassed maximum depths of 2-3 m.

Habitat-scale tracking was conducted using an acoustic positioning system, Vemco Positioning System (VPS). Similar to other acoustic positioning systems, VPS utilized receivers with overlapping detection ranges to triangulate individual fish positions (Espinoza et al. 2011a). Synchronization transmitters ("synctags"; Vemco V13-1H) programmed with a random 500-700 second delay were co-located with each receiver to correct for time drift of the receivers' internal clocks. Two stationary control transmitters (Vemco V9-1x) were deployed within the array (one in the inner lagoon and one in the open bay) for the duration of the study to monitor diel trends in detection efficiency of the system. The habitat-scale array was in place for one month, with tagging initiated on June 11, 2013.

Tagging protocols were identical across species and locations throughout the study. Red drum and spotted seatrout were captured via hook-and-line and placed in coolers supplied with pure oxygen prior to tagging. Surgical procedures followed the methods of Robillard et al. (2015). Transmitters were inserted through a small incision parallel to the linea alba between anal and pelvic fins, and one or two interrupted stitches with absorbable sutures (4-0 Ethicon vicryl) were used to close the wound. Transmitters, sutures, and surgical tools were disinfected in a benzalkonium chloride solution prior to use. Fish total length (TL) was measured to the nearest millimeter, and Hallprint dart tags offering anglers a reward for reporting recaptured fish were applied at the junction of first and second dorsal fins. Individual fish were observed for at least 15 minutes following surgery and released only if they exhibited normal behavior throughout.

Individuals caught, tagged, and released at the habitat-scale array at Mud Island in June 2013 (red drum n = 14; spotted seatrout n = 15) were implanted with transmitters (Vemco V9-1H) programmed with a random 100-180 second delay for the first 20 days, which then converted to a random 400-500 second delay (estimated battery life: 500 days). No additional spotted seatrout were tagged following the initial release group. Further tagging focused on red drum only, which were caught, tagged, and released at 12 additional locations in 2013 to distribute sampling effort (Figure 1). Red drum released at these locations in July (n = 20) and November/December (n = 20) were implanted with Vemco transmitters (Vemco V9-1H) programmed with a random 400-500 second delay (estimated battery life: 530 days). Fish were assigned a year class based on age-length keys reported by Porch et al. (2002) for red drum and Nieland et al. (2002) for spotted seatrout (Appendix 1). Age classes were designated based on estimated age at the end of the calendar year in which individuals were tagged.

Data analysis

Two methods for position estimation were employed to assess habitat-scale movement: VPS positioning and short-term center of activity (COA). VPS positioning was performed using time-difference-of-arrival analysis, requiring reception of the same transmission by three or more receivers to triangulate fish position. VPS positions were filtered by horizontal positioning error (HPE), a unitless measure of positioning error derived from synctag positioning success and local environmental conditions affecting the speed of sound (e.g., temperature, salinity). Only VPS positions with HPE < 10 were used for statistical analysis. These values corresponded to actual position errors of approximately 2 m or less based on comparing HPE to known positioning error for synctags and reference tags (1.26 ± 0.03 m, mean ± SE) for the duration of the study. Hourly COA positions were estimated by calculating the arithmetic means of the latitude and longitude of the receiver(s) detecting a fish during each hour period as described by Simpfendorfer et al. (2002). In contrast to VPS positioning, which only includes signal transmissions detected by three or more receivers, COA positioning incorporates all signal transmissions recorded by the array. Detections recorded in the first two hours after releasing the fish were excluded from VPS and COA positioning to account for post-surgery behavioral acclimation. For temporal analysis, VPS positions were binned by diel stage: day, night, or crepuscular, defined as one hour before and one hour after sunrise and sunset. Sunrise and sunset information for Port Aransas, Texas was downloaded from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service, and tidal information for Port Aransas was downloaded from the NOAA Tides and Currents database.

Core use areas based on 50% fixed kernel densities were estimated using ArcGIS 10.0 (ESRI, Redlands CA), and a 50 m search radius was used for kernel construction. For each individual fish, separate core use areas were constructed using VPS and COA positions, respectively. Habitat use was analyzed using Euclidean distance-based analysis (EDA; Conner and Plowman 2001), and a classification-based method, compositional analysis (CA; Aebischer et al. 1993). Both are widely used tests with different interpretations of habitat selection, and were chosen with the goal of obtaining a thorough evaluation of habitat use. The minimum convex polygon that included all VPS positions and core use kernels was used as the boundary delineating available habitat for EDA and CA analyses.

The EDA ratios were estimated using the distances from VPS positions to each available habitat type compared against the distances to these habitat types for a distribution of 1000 random points (Conner and Plowman 2001). Boundaries between all habitat types ("habitat edges") were merged and categorized as a distinct habitat type for this analysis. Ratios were calculated as the mean observed distance (from fish positions) divided by the mean expected distance (from random points) to each habitat type. A unique EDA ratio was calculated for each habitat type for each fish, retaining the individual as the experimental unit. If habitat use is completely random, the EDA ratio is expected to be equal to one, with values > 1 indicating positions farther from a habitat type than expected ("less use") and values < 1 indicating positions closer to a habitat type than expected ("greater use"). Multivariate analysis of variance (MANOVA) was used to determine if mean EDA ratios for each habitat type within species differed from a vector of 1's with a length equal to the number of habitat types investigated (4)(Conner and Plowman 2001). If overall habitat use was nonrandom as indicated by a significant MANOVA test, analysis of variance (ANOVA) was employed within species to test each habitat type specifically for disproportionate use by comparing its mean EDA ratio to 1. This analysis was not conducted using COA positions because they lack the spatial and temporal resolution appropriate for testing specific habitat association. The level of significance (α) was set at 0.05 for all statistical testing.

Compositional analysis was used to compare the composition of habitat types present in the core use area (derived from VPS and COA positions, respectively) of each fish to the composition of available habitat within the study area. Since the composition of habitat components summed to 1, improved log-ratio analysis was used to avoid the unit-sum constraint (Aebischer et al. 1993). Zero values for unused habitats cannot be included in log-ratio analysis, and therefore zeroes were replaced with 0.001%, a value less than the lowest nonzero proportion of habitat use (Aebischer et al. 1993). The null hypothesis of random overall habitat use was tested using MANOVA. If results showed nonrandom overall habitat use, a ranking matrix of pairwise habitat comparisons based on univariate t-tests of 999 randomizations of the data was used to order habitats by use.

Total habitat-scale tracking duration was calculated as the total number of days between the first and last detections for each fish, inclusive of the days in which those detections occurred. Residency was defined as the number of days an individual was detected at least twice. Two sample t-tests were used to test for differences in total tracking duration and residency between species. Rate of movement (ROM) was calculated as the linear distance between VPS positions divided by time elapsed. Rates were only calculated if successive positions occurred within a 17 minute period, the time interval required to encompass two successive detections following transmitter conversion to a random delay of 400 to 500 seconds (20 days post release). This restriction reduced the possibility of underestimating distances traveled due to missing locations. Because ROM data for each diel period existed only for a limited number of individuals, these data were pooled by species. Water depth at each VPS and COA position was calculated by correcting interpolated depths derived from field observation by predicted tidal height (Furey et al. 2013), and two sample t-tests were used to test for differences between species using both VPS and COA positions.

Total bay-scale tracking duration was calculated as the total number of days between release and the last known fish position (detection or angler report). Detections from the habitat-scale array at Mud Island were included in total tracking duration but excluded from bay-scale detection totals, and individual fish were only included in analyses if they were detected at least 10 days post release. Two sample t-tests were used to test for differences in tracking duration and number of detections between age classes of red drum. For each month, individuals were classified as staying or moving. An individual was categorized as staying if detected by only one receiver during the month, with a minimum span of at least seven days between the first and last detection. An individual was considered moving if detected by more than one receiver during the month or detected by a receiver that was different than its most recent position (receiver or release site). If individuals met either of these criteria in the same calendar month during different years, both outcomes were included in staying or moving totals, respectively. Monthly movement calculations only included fish that were detected moving between bay-scale receivers.

Distance traveled between fish positions was estimated using the cost path function in ArcGIS 10.0, which calculated the shortest distance that eliminated the possibility of movement over land (through water only). Total distance traveled at the bay scale was estimated as the sum of these movement distances for each individual. Final displacement was also calculated using the cost path function, and estimated as the shortest distance (through water only) between release location and the last known fish position. Two sample t-tests were used to test for differences in total distance traveled and final displacement between age classes of red drum. The proportion of detections that occurred at an individual's "home receiver," defined as a receiver located within 1 km of an individual's release site, was calculated only for individuals released at such proximity to a receiver. Both receivers at Mud Island were considered home receivers for red drum and spotted seatrout released at that site.

RESULTS

Habitat scale

A total of 48,292 detections were recorded by the habitat-scale array at Mud Island: 13,433 for red drum and 34,859 for spotted seatrout (Appendix 1). Detection data yielded 1,540 VPS positions (170 red drum and 1,370 spotted seatrout) and 3,026 hourly COA positions (829 red drum and 2,197 spotted seatrout). After filtering HPE, 167 red drum and 1,310 spotted seatrout VPS positions were included in analyses. Overall, the majority of VPS positions for red drum were located over seagrass (52.7%), with lower occurrence over bare substrate (29.9%) and oyster reef (17.4%). More than half of the VPS positions for spotted seatrout were also located over seagrass (51.9%); however, high occurrence over bare substrate (48.0%) was also observed for this species. Spotted seatrout VPS positions over oyster reef (0.1%) were markedly lower than all other habitats (Figure 2). Red drum COA positions indicated more even use of seagrass (40.7%) and bare substrate (47.0%). Fewer COA positions were located over oyster reef (12.3%), consistent with observations for VPS positions. Unlike VPS results, COA positions for spotted seatrout indicated higher occurrence over bare substrate (77.1%) with lower use of seagrass (22.2%); occurrence of spotted seatrout COA positions over oyster reef (0.7%) was similarly low (Figure 2).

Analysis of EDA ratios indicated nonrandom habitat use by both red drum (MANOVA; $p < 0.05$) and spotted seatrout (MANOVA; $p < 0.01$). Red drum were found significantly closer than expected to seagrass (EDA = 0.39; ANOVA; $p < 0.05$), oyster reef (EDA = 0.40; ANOVA; $p < 0.01$), and habitat edges (EDA = 0.41; ANOVA;

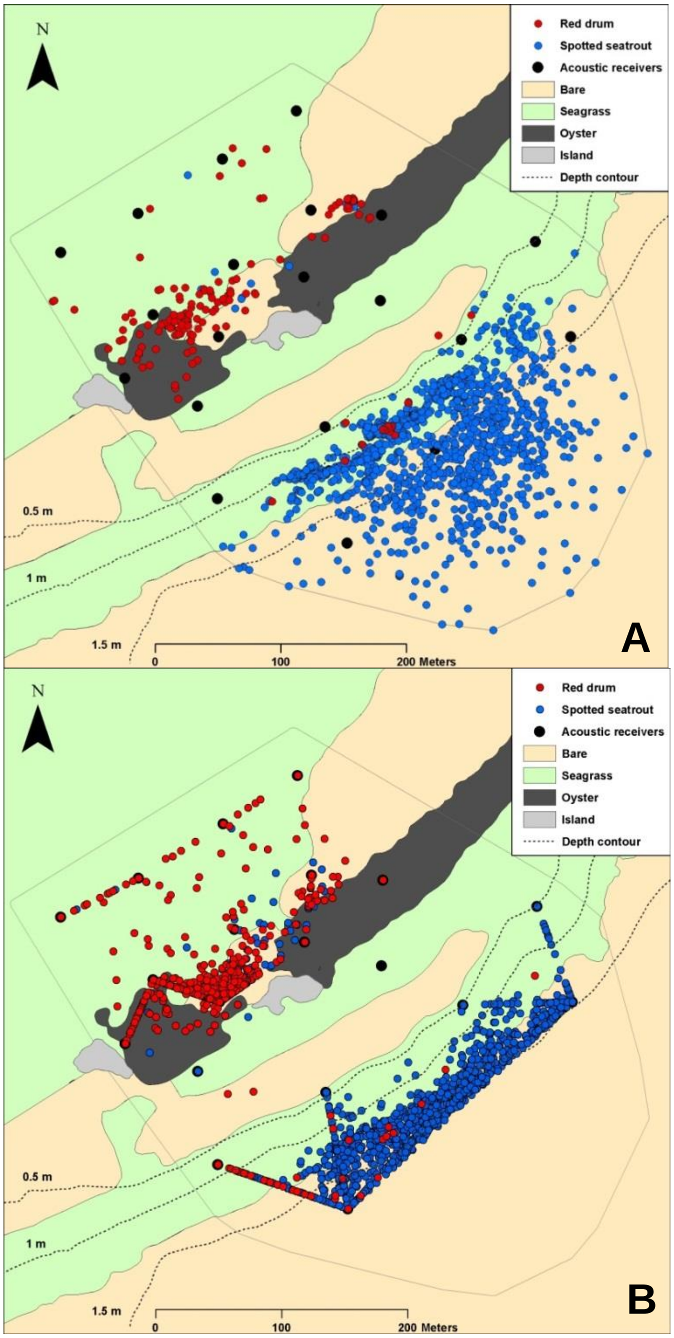

Figure 2. Map of the habitat-scale tracking array at Mud Island (Aransas Bay, TX) and the distributions of A) Vemco positioning system (VPS) positions and B) short-term center of activity (COA) positions of late juvenile red drum and spotted seatrout. Dashed lines represent water depth contours, and the solid line represents the boundary delineating available habitat for analysis of habitat selection.

$p < 0.01$) (Figure 3). Mean distance of red drum to bare substrate was not significantly different from random (EDA = 0.77; ANOVA; $p > 0.05$). Spotted seatrout were found significantly closer than expected to bare substrate (EDA = 0.44; ANOVA; $p < 0.01$) and significantly farther than expected from oyster reef (EDA = 1.44; ANOVA; $p < 0.05$). Mean distance of spotted seatrout to seagrass (EDA = 0.80; ANOVA; $p > 0.05$) and habitat edges (EDA = 0.80; ANOVA; $p > 0.05$) were not significantly different from random. Compositional analysis of VPS positions indicated that overall habitat use was random for red drum (MANOVA; $p > 0.05$), and nonrandom for spotted seatrout (MANOVA; $p < 0.05$), and spotted seatrout use of seagrass and bare substrate was significantly greater than that of oyster reef (t-test; $p < 0.05$). Compositional analysis of COA positions indicated nonrandom habitat use by both red drum (MANOVA; $p < 0.05$) and spotted seatrout (MANOVA; $p < 0.01$; Table 1). Red drum use of seagrass and oyster reef was significantly greater than that of bare substrate (t-test; $p < 0.05$), and spotted seatrout use of bare substrate was significantly greater than seagrass (t-test; $p < 0.05$), which was in turn significantly greater than oyster reef (t-test; $p < 0.05$; Table 1).

Apart from habitat type, water depth was another parameter that influenced habitat use. Mean water depth differed significantly between red drum and spotted seatrout based on both VPS (t-test; $p < 0.01$) and COA positions (t-test; $p < 0.01$). Mean water depth estimates for red drum positions (VPS: 50.6 ± 8.5 cm; COA 53.4 ± 5.3 cm) were shallow compared to spotted seatrout (VPS: 143.6 ± 9.7 cm; COA (132.1 ± 10.5 cm) (Figure 4). Moreover, red drum were more frequently detected in the inner lagoon (VPS: 82.6 ± 12.7%; COA: 85.5 ± 6.2%) than the open bay side of the array (VPS: 17.4

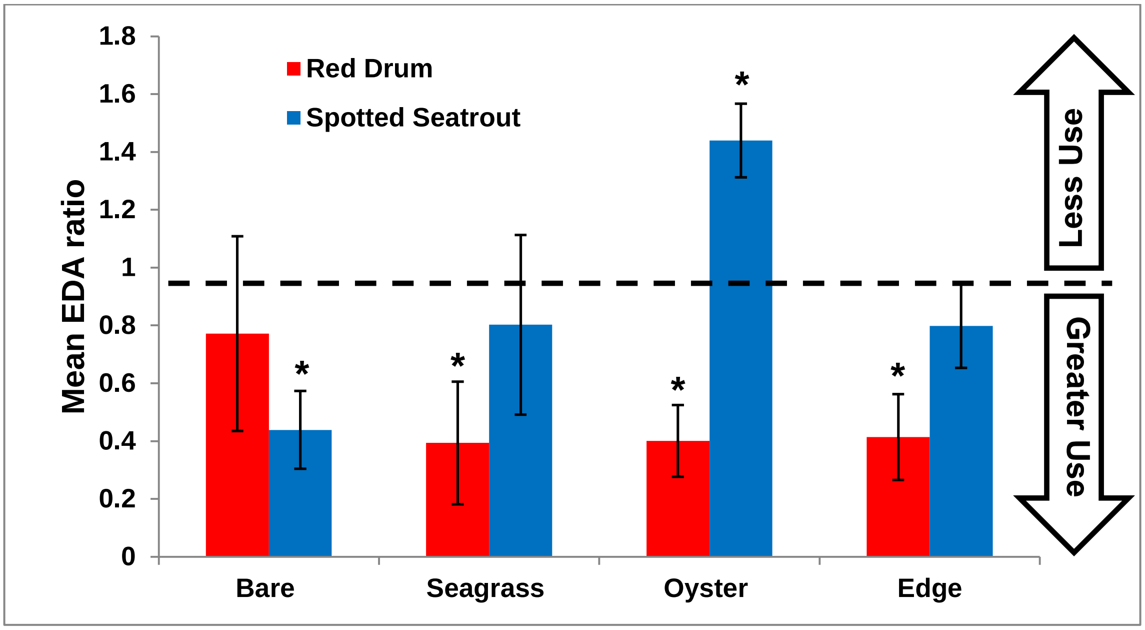

Figure 3. Euclidean distance-based analysis (EDA) of habitat selection by late juvenile red drum and spotted seatrout. Mean EDA ratios compared distance to each habitat type for VPS positions against distance to each habitat type for a distribution of 1000 random points. EDA ratio = 1 (represented by dashed line) indicates habitat use is random, EDA ratio < 1 indicates relatively greater use, and EDA ratio > 1 indicates relatively less use. Asterisks represent significant difference from expected use of each habitat type, and error bars represent ± one standard error of the mean.

Table 1. Rank order of habitat use based on compositional analysis (CA) of 50% core use kernels. Core use kernels were derived using Vemco positioning system (VPS) and center of activity (COA) position estimations. MANOVA was used to determine if overall habitat use was random or nonrandom. If overall habitat use was found to be nonrandom, use of specific habitat types was ranked by univariate t-tests of 999 randomizations of the data. Habitats that share an underline were deemed to be used equally.

	Less use <-----------> Greater Use
Red drum	
VPS kernels	habitat use random
COA kernels	bare substrate < oyster reef; seagrass
Spotted seatrout	
VPS kernels	oyster reef < seagrass; bare substrate
COA kernels	oyster reef < seagrass < bare substrate

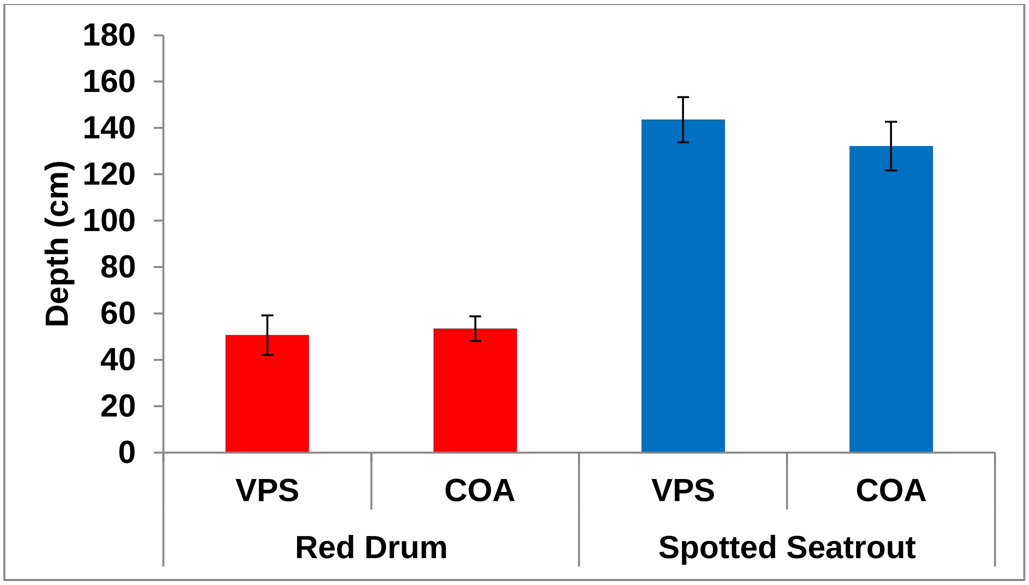

Figure 4. Comparison of mean water depth of positions estimated using Vemco positioning system (VPS) and short-term center of activity (COA) for late juvenile red drum and spotted seatrout. Error bars represent ± one standard error of the mean.

± 12.7%; COA: 14.5 ± 6.2%). In contrast, spotted seatrout rarely used the inner lagoon (VPS: 3.7 ± 3.4%; COA: 26.1 ± 9.1%) and were commonly found on the open bay side of the array (VPS: 96.3 ± 3.4%; COA: 73.9 ± 9.1%).

Tracking duration at the habitat scale was 20.4 ± 2.3 days (mean ± SE) for red drum and 23.4 ± 1.9 days for spotted seatrout, and mean residency was 8.8 ± 1.9 days for red drum compared to 13.1 ± 2.8 days for spotted seatrout. Mean number of revisits to the array following absences greater than 24 hours was identical for red drum (2.4 ± 0.6) and spotted seatrout (2.4 ± 0.8). Total tracking duration, residency, and revisits all were statistically similar between the two species (t-test; $p > 0.05$).

Temporal variability in habitat use and movement rates was observed for red drum and spotted seatrout. Detections for both species were greatest during the morning, between 06:00-09:00 h for red drum and 04:00-07:00 h for spotted seatrout (Figure 5). Habitat use of both species was influenced by time of day. The proportion of red drum VPS positions over bare substrate was greatest during the day (46.2%) and lowest at night (13.9%), while the proportion over seagrass was greatest at night (75%) and lowest during the day (36.9%). Spotted seatrout VPS positions were almost exclusively located over seagrass during the day (98.0%) and shifted to bare substrate at night (80%; Figure 6). Both species also exhibited diel variability in ROM, which was lowest during the day (red drum: 1.39 m min^{-1}; spotted seatrout: 0.95 m min^{-1}) and greatest at night (red drum: 2.72 m min^{-1}; spotted seatrout 3.4 m min^{-1}). Crepuscular habitat use and ROM was intermediate between that of day and night in each aforementioned comparison.

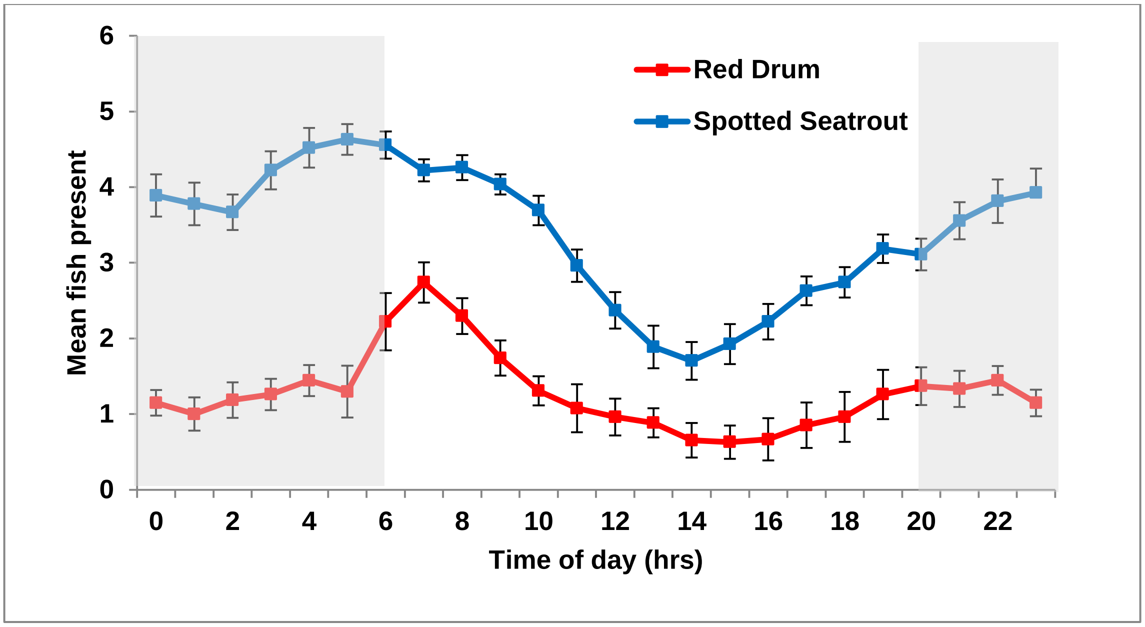

Figure 5. Mean hourly presence (detected by any receiver) of late juvenile red drum and spotted seatrout in the habitat-scale array. Shaded area represents night hours, and error bars represent ± one standard error of the mean.

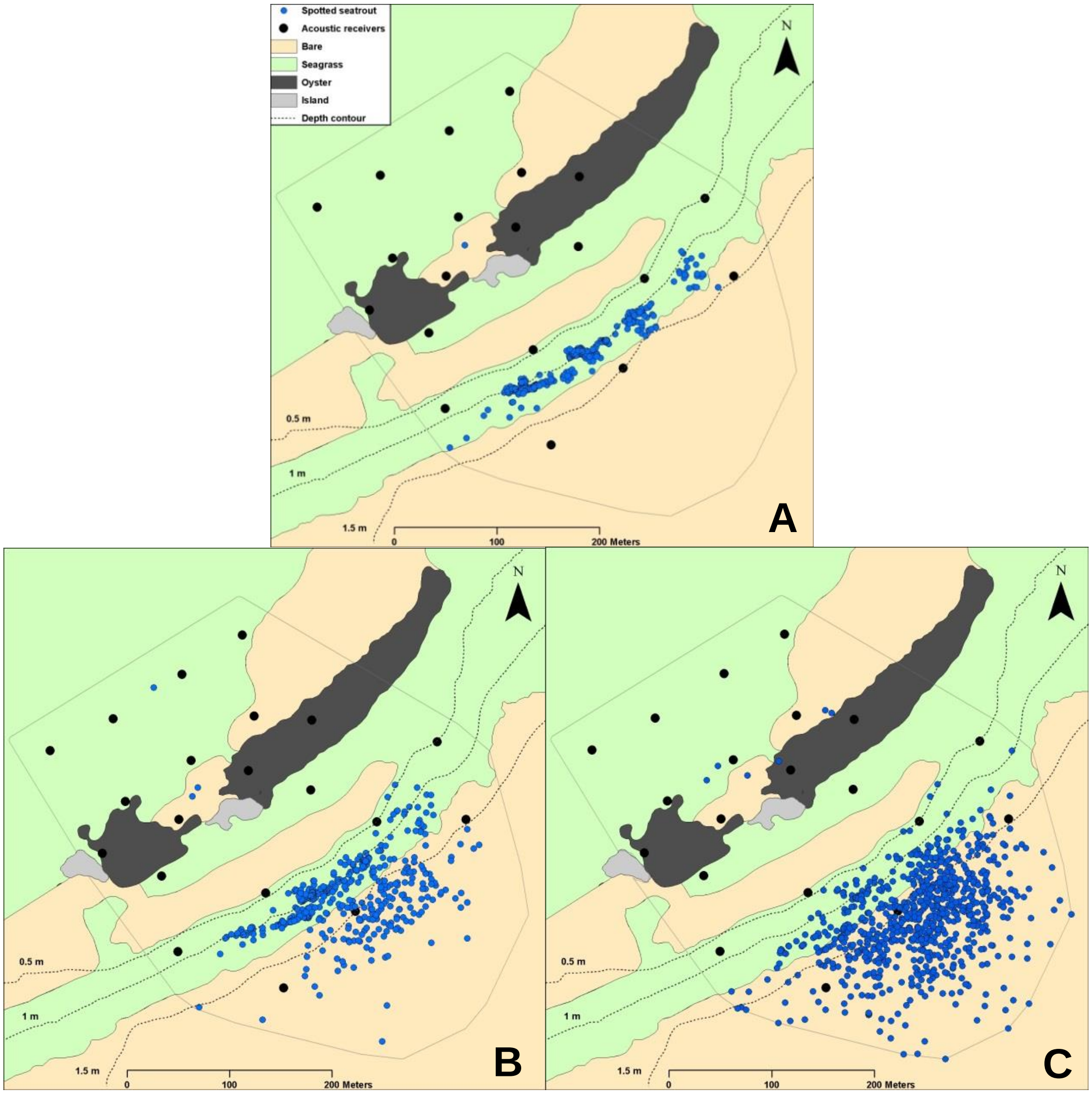

Figure 6. Vemco positioning system (VPS) positions of late juvenile spotted seatrout categorized by A) day, B) crepuscular, and C) night periods. Crepuscular period is defined as one hour before to one hour after sunrise and sunset. Substantially more VPS positions were recorded per diel period for spotted seatrout (436.7) compared to red drum (55.7).

Bay scale

At the bay-scale, 44 of 54 (81.5%) red drum and 13 of 15 (86.7%) spotted seatrout were detected at least 10 days post release. After filtering, a total of 58,645 detections were recorded for red drum and 3,175 for spotted seatrout (Figure 7). Mean detections were 1332.8 ± 550.7 for red drum and 244.2 ± 93.9 for spotted seatrout, and 1973.8 ± 1296.1 for age-1 compared to 1058.4 ± 572.1 for age-2 red drum. Differences in detections between age classes of red drum were not statistically significant (t-test; $p > 0.05$; Table 2). Tracking duration at the bay-scale was 246.9 days ± 22.5 for red drum and 153.5 days ± 27.7 for spotted seatrout. Bay-scale tracking duration was 272.9 days ± 45.1 for age-1 and 236.1 days ± 26.0 for age-2 red drum, and this difference was not statistically significant (t-test; $p > 0.05$; Table 2). Maximum bay-scale tracking duration for spotted seatrout was only nine calendar months (none detected after March 2014), while 16 (29.6%) red drum were tracked for nine or more calendar months. Seven (15.9 %) red drum were tracked for a period of 15 or more calendar months.

Seasonal movement patterns were evident for individuals of both species, with directed movements detected during winter and spring. Mean distance traveled by month (including moving individuals only) was greatest for red drum in February (20.8 km), March (16.5 km), and April (14.6 km; Figure 9), and greatest for spotted seatrout in December (15.0 km), January (21.3 km), and February (15.0 km; Figure 9). While several individuals were detected at a single bay-scale receiver from May to August, no individual of either species was detected moving between bay-scale receivers (with the exception of the receivers at Mud Island) during these months (Figure 8). Maximum

Table 2. Summary of bay-scale tracking data for A) late juvenile red drum and spotted seatrout and B) red drum age classes. Individuals were only included if they were detected at least 10 days post release, so 44 red drum (age-1 n = 11; age-2 n = 33) and 13 spotted seatrout were included in analysis. Tracking duration was calculated from release until the last recorded fish position, and total distance was calculated as the sum of minimum distances (through water) between receivers detecting each individual. Final displacement was calculated as the minimum distance (through water) between the release site and the last recorded fish position (detection or angler report). Values reported are minimum (min), maximum (max), mean, and standard error (SE). Age classes were designated based on estimated age at the end of the calendar year in which individuals were tagged.

A)

	Red drum			**Spotted seatrout**		
	Min	**Mean (SE)**	**Max**	**Min**	**Mean (SE)**	**Max**
Detections	3	1332.8 (550.7)	17087	30	244.2 (93.9)	895
Tracking duration (days)	11.8	246.9 (22.5)	522.7	13.0	153.5 (27.7)	267.3
Total distance (km)	0	11.9 (2.8)	72.4	0	15.5 (6.7)	68.6
Final displacement (km)	0	3.0 (0.8)	31.1	0	1.6 (0.9)	11.1

B)

	Age 1			**Age 2**		
	Min	**Mean (SE)**	**Max**	**Min**	**Mean (SE)**	**Max**
Detections	11	1973.8 (1296.1)	16446	3	1064 (571.9)	17087
Tracking duration (days)	41.6	272.9 (45.1)	522.7	11.8	236.1 (26.0)	498.5
Total distance (km)	0	20.3 (6.6)	72.4	0	10.8 (2.8)	69.6
Final displacement (km)	0	5.7 (2.5)	31.1	0	1.8 (0.4)	8.2

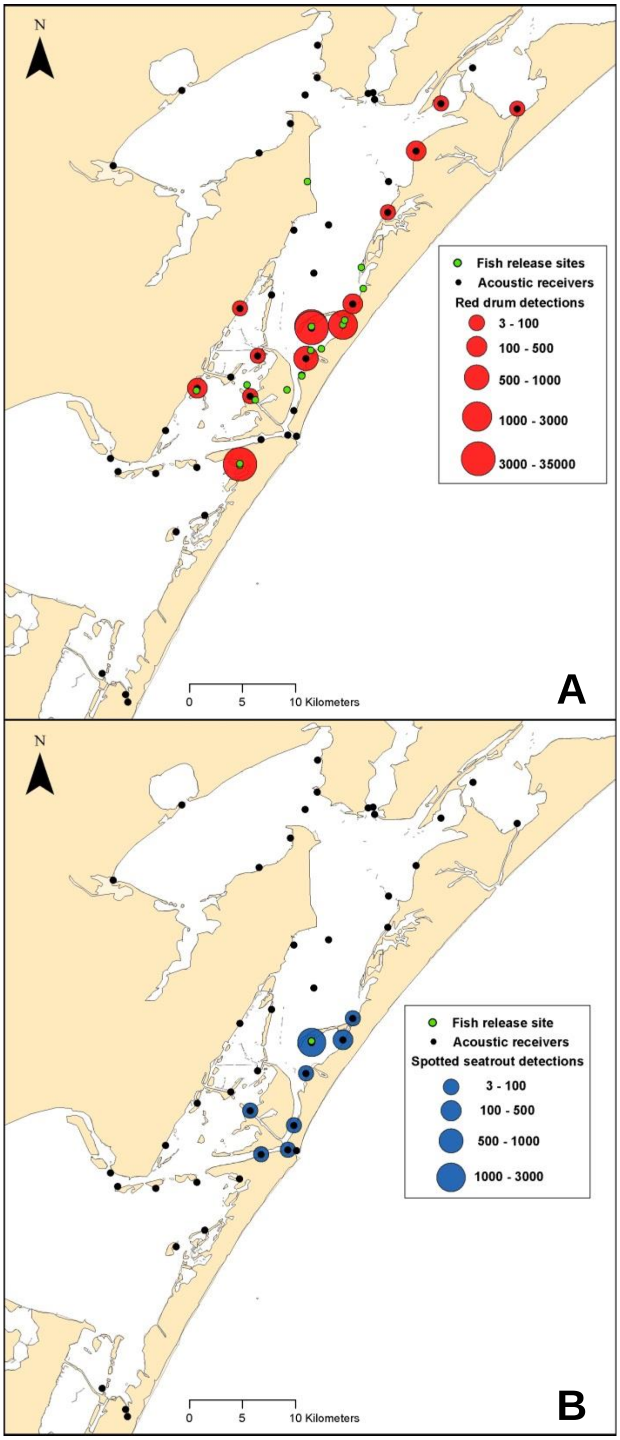

Figure 7. Total detection quantities from bay-scale acoustic receivers. Detections were pooled by species for A) late juvenile red drum (n = 44) and B) late juvenile spotted seatrout (n = 13).

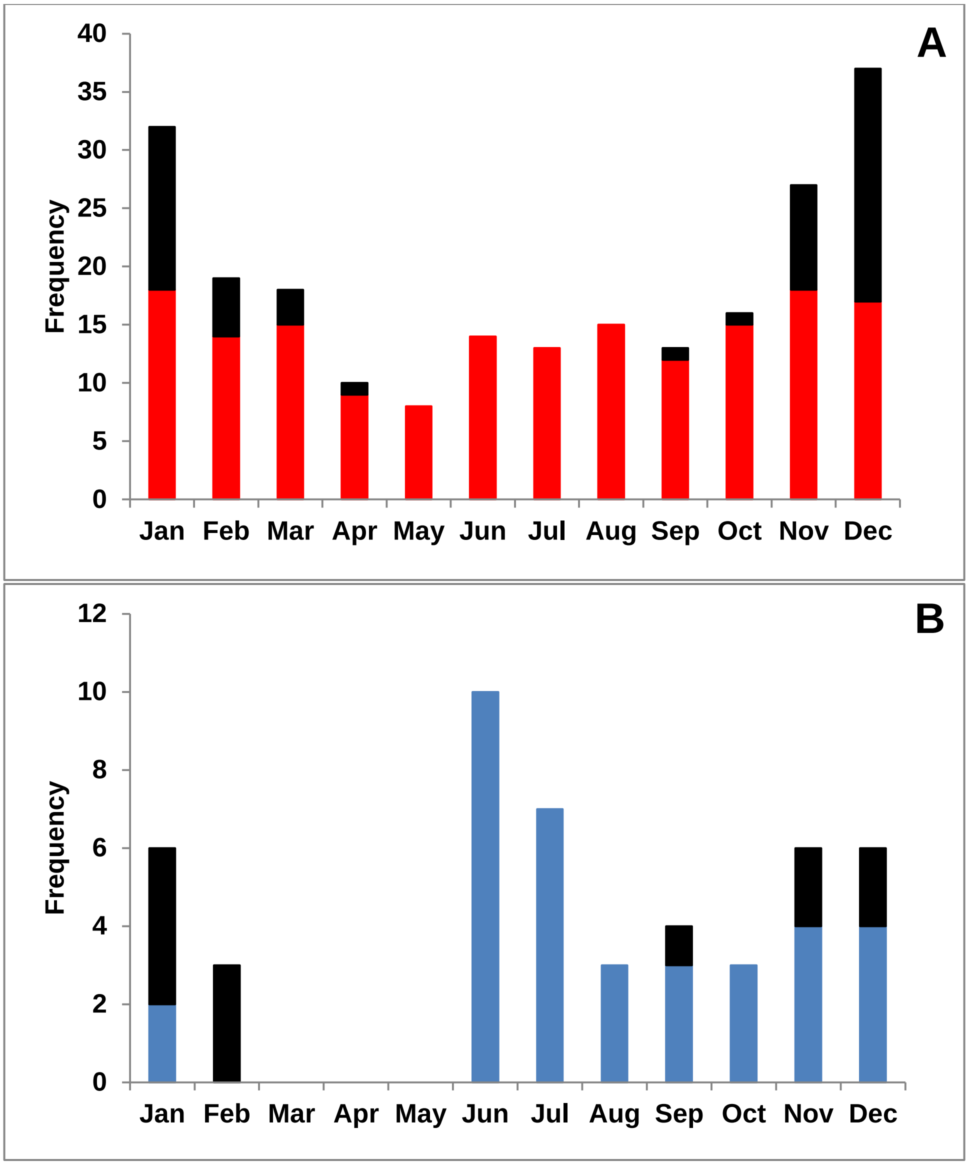

Figure 8. Frequency of individuals “staying” or “moving” at bay scale receivers by month for A) late juvenile red drum and B) late juvenile spotted seatrout. Individuals staying were represented by red bars (red drum) or blue bars (spotted seatrout), and individuals moving were represented by black bars for both species. Note the difference in axis values. An individual was considered staying if it was detected by only one receiver during the month, with a minimum span of at least seven days between the first and last detection. An individual was considered moving if it was detected by more than one receiver during the month, or it was detected by a receiver which was different than its most recent position (receiver or release site). If an individual met either of these criteria in the same calendar month during different years, both outcomes were included in staying or moving frequencies, respectively.

total distance traveled by an individual was 72.4 km for red drum and 68.6 km for spotted seatrout. Minimum distance traveled by certain red drum and spotted seatrout was 0, indicating that all detections for these individuals were from a receiver at the release location. Overall mean distance traveled was 11.9 ± 2.8 km for red drum and 15.5 ± 6.7 km for spotted seatrout. Overall mean distance traveled was 20.3 ± 6.6 km for age-1 compared to 8.4 ± 2.8 km for age-2 red drum, which was not significantly different between age classes (t-test; $p > 0.05$; Table 2).

Movement away from the release location was limited for both species, with mean final displacement distances of 3.0 ± 0.8 km for red drum and 1.6 ± 0.9 km for spotted seatrout. Mean final displacement was greater for age-1 (5.7 ± 2.5 km) compared to age-2 (1.8 ± 0.4 km) red drum, though the difference was not statistically significant (t-test; $p > 0.05$; Table 2). For individuals of both species released less than 1 km from a home receiver (red drum $n = 26$; spotted seatrout $n = 13$), the proportion of detections recorded at the home receiver was high (red drum 89.7 ± 5.2%; spotted seatrout 85.6 ± 4.9%).

DISCUSSION

Habitat-scale movement was species-specific and influenced by habitat type, water depth, and diel cycle. Late juvenile red drum were commonly found over each habitat type (seagrass, oyster reef, bare substrate) present at the Mud Island array, and EDA and CA indicated higher use of seagrass and oyster reef. This is consistent with previous investigations, which showed red drum using a variety of habitat types but selecting structured habitats such as seagrass and oyster reef (Bacheler et al. 2009; Fodrie et al. 2015; Dance and Rooker in review). In addition to a general preference for structured habitat, the current study also demonstrated that red drum were commonly associated with habitat edges or boundaries between two different habitat types, a finding also observed by Dance and Rooker (in review) for red drum in Christmas Bay, Texas. These edges are often associated with increased prey abundance (Bostrom et al. 2006), and therefore this behavior may enhance foraging opportunities for red drum.

Similar to red drum, EDA and CA indicated that late juvenile spotted seatrout also preferred specific habitats, with individuals commonly associated with seagrass and bare substrate. Association with seagrass by early juvenile spotted seatrout is well established, (McMichael and Peters 1989; Rooker et al. 1998; Neahr et al. 2010; Flaherty-Walia et al. 2015), and my results indicate that seagrass continues to be important habitat for spotted seatrout during the late juvenile stage. Seagrass and other types of submerged aquatic vegetation are known to enhance foraging opportunities of juvenile fishes (Gillanders 2006), while also serving as visual and physical barriers to predators (Main 1987), thereby lowering encounter and capture rates (Heck and Orth 2006). Moreover, a recent study by Wilson et al. (2013) indicated that seagrass attenuates high frequency sounds used to echolocate prey by higher order consumers such as dolphins that frequent the estuary and are known to feed on sciaenids (Gannon and Waples 2004). Thus, it is not surprising that spotted seatrout continue to benefit from this habitat during the late juvenile period. Apart from seagrass, oyster reef represents another structured habitat used by estuarine fishes, including certain sciaenids (Stunz et al. 2010); however, spotted seatrout in the Mud Island array rarely associated with shallow oyster reef. In fact, spotted seatrout were more commonly found over bare substrate than oyster reef, which is likely more reflective of preferences for water depth rather than habitat type because of the shallow nature of these reefs.

Habitat-scale tracking results also showed a high degree of spatial separation between late juvenile red drum and spotted seatrout, which may be indicative of habitat partitioning. Habitat partitioning in fishes has previously been documented for species with overlapping home ranges and resource utilization patterns (Werner et al. 1977; Kinney et al. 2011; Knickle and Rose 2014). In this case, red drum and spotted seatrout at Mud Island occupied different depth zones within the array. The majority of red drum positions were located in the inner lagoon (depth < 0.5 m), while most of the spotted seatrout positions were located in the open bay (depth > 0.5 m). Mean water depth of areas used by spotted seatrout was greater than that of red drum by approximately a meter (Figure 4), which is substantial given the limited scope of water depths (0.5-3.0 m) within the array. These findings indicate that water depth influences habitat use of both species and likely plays a role in ecosystem connectivity within estuarine seascapes comprised of multiple habitat types. It is possible that the ontogenetic and seasonal shifts in water depth preference occur for both species, and thus precaution should be exercised when interpreting water depth use patterns from late juveniles during summer months.

Spatial partitioning at the habitat scale by late juvenile red drum and spotted seatrout may allow each species to target specific prey fields, potentially minimizing overlap in their diets (Ross 1986). Both species are opportunistic feeders with diets mainly composed of fishes and crustaceans. Although their diets overlap to some degree (Llanso et al. 1998), red drum derive a greater contribution from macroinvertebrates including crabs, shrimps, and polychaete worms while spotted seatrout are largely piscivorous (Overstreet and Heard 1978; Llanso et al. 1998; Scharf and Schlicht 2000). Macroinvertebrates are commonly associated with seagrass and oyster reef (Attrill et al. 2000; Stunz et al. 2010), while small baitfish often avoid shallow water due to predation threat (Baker and Sheaves 2007), suggesting that red drum and spotted seatrout habitat partitioning based on water depth is driven by foraging preferences. Given that the relative contribution of fishes and invertebrates to red drum diets (Scharf and Schlicht 2000) and the composition of shallow estuarine communities (Rakocinski et al. 1992) both vary seasonally, it is unclear whether spatial partitioning at the habitat scale is maintained as prey distribution and environmental conditions fluctuate.

Temporal variability in habitat use and movement is well-documented and primary linked to foraging and/or avoiding predators (Werner et al. 1983, Helfman 1986, Becker and Suthers 2014). Strong diel trends emerged for late juvenile spotted seatrout, with individuals almost exclusively associated with seagrass (VPS: 98%) during the day before shifting primarily to bare substrate (VPS: 80%) at night. Moreover, ROM was markedly lower during the day (0.95 m min^{-1}) compared to night (3.4 m min^{-1}), with increased ROM or greater activity at night possibly linked to foraging (Reebs 2002). Peak feeding at night has previously been observed for sciaenids (Facendola and Scharf 2012), and the distinct increase in nocturnal activity revealed by ROM indicates that this was likely for spotted seatrout in the current study. Late juvenile red drum ROM followed the same trend as spotted seatrout, but unfortunately the interpretation of diel variability for red drum was limited by low sample size, especially at night. Foraging efficiency can be lower at night (Fraser and Metcalfe 1997), and thus nocturnal feeding by spotted seatrout may be a mechanism to minimize predation risk. Habitat use (VPS: 63% seagrass, 37% bare substrate) and ROM (2.6 m min^{-1}) for spotted seatrout during crepuscular periods was intermediate to observations during the day and night, and this may be indicative of the transition period when individuals are moving from daytime resting sites to nocturnal foraging areas.

This study employed complementary approaches to estimate fish position at the habitat scale, and even though the spatial and temporal resolution of the positioning methods differed, both estimated similar distributions (Figure 2). Because VPS requires simultaneous detections by three or more receivers, it was assumed that this positioning method would provide the most accurate estimates for characterizing habitat-scale associations (Andrews et al. 2011). The challenge for VPS at this particular site was common depths < 1 m, which limits detection ranges and therefore opportunities for triangulation (Gjelland and Hedger 2013). In contrast, COA allowed for the inclusion of all recorded detections, generating a more holistic image of each fish's space use. The presumed limitation of COA is lower spatial resolution, because receiver locations (latitude and longitude) for all detections within a given period of time are used to approximate fish position. Even though detections were averaged over the span of an hour, COA often estimated exact receiver positions or positions along a line between receivers. Each positioning approach carried limitations in the context of this study; nevertheless, VPS and COA estimates of habitat use and water depth were similar within species and allowed analyzation of multiple spatial and temporal resolutions by testing specific habitat associations and general space use.

Habitat-scale movement was analyzed using both distance-based (EDA) and classification-based (CA) methods to contrast results from both approaches. As a distance-based analysis, EDA can account for the influence of multiple habitat types as well as habitat edge; however, it can be affected by the spatial arrangement of habitat patches (Bingham et al. 2010). Compositional analysis is more robust to effects from habitat arrangement, but can be affected by misclassification due to positioning error (Conner et al. 2003). In this study, EDA revealed close association to habitat edge by red drum, which cannot be evaluated with CA. However, EDA also indicated that spotted seatrout avoided oyster reef, but interpretation of this finding requires caution due to oyster reef only being present in the shallow depth zone of the array. Overall, differences between the two approaches were minor. For red drum, CA showed random habitat use, while both CA and EDA revealed nonrandom habitat use characterized by high use of seagrass and oyster reef. For spotted seatrout, both EDA and CA revealed nonrandom overall habitat use which was high for bare substrate and low for oyster reef, with classification of seagrass differing slightly. Each approach provided a distinct analysis of habitat selection, yet findings of the two were generally in accord, strengthening the interpretation of habitat use.

Bay-scale movement of late juvenile red drum and spotted seatrout was primarily restricted to small regions within bays, suggesting high residency. Mean final displacement of red drum and spotted seatrout was low (< 5 km), and many individuals were detected in the same area for several consecutive months. The mean proportion of detections occurring at the home receiver was very high (85-90%) for each species. These results are consistent with previous otolith chemistry (Patterson et al. 2004; Rooker et al. 2010) and tagging (Adams and Tremain 2000, Baker and Matlock 1993; Bacheler et al. 2009a) studies, which indicate that the degree of inter-bay connectivity is low for spotted seatrout and possibly only marginally higher for red drum, with exchanges among estuaries unlikely at distances greater than 100 km. High residency and limited movement by both species suggests that conditions within the home estuary (e.g. habitat quality, environmental parameters, and fishing pressure) likely have the greatest impact on local populations, and monitoring these conditions is critical to sustaining the nursery function of areas within bays. In turn, it appears that population dynamics for late juveniles of both species will be influenced by local production with minimal contributions from other estuarine systems, and thus management of both species should occur at smaller spatial scales than currently used by state agencies (Rooker et al. 2010).

Directed bay-scale movement of late juvenile red drum and spotted seatrout followed a seasonal pattern, occurring primarily during winter and early spring (December - March). This contrasts previous reports of greatest red drum movement during fall (Bacheler et al. 2009b) and limited spotted seatrout movement during winter (Ellis 2014), but aligns temporally with observations of red drum leaving shallow habitats in December before returning in March or April (Stewart and Scharf 2008). Red drum growth is positively associated with water temperature (Lanier and Scharf 2007), and thus it is possible that increased bay-scale movement in the winter was driven in part to seek thermal refuge, because water temperatures in the MANERR system were lowest between December and March. However, during these months many individuals did not leave areas in which they were consistently detected during other seasons; although, it is unclear if habitat-scale movement was altered. As a result, additional research is needed to identify factors influencing directed bay-scale movement and its timing and magnitude, which will lead to a greater understanding of the pathways of connectivity for red drum and spotted seatrout present in the MANERR and associated waters.

CONCLUSIONS

Seascape structure has been implicated as an important driver of ecosystem connectivity for estuarine fishes (Bostrom et al. 2011), and findings from this study clearly demonstrate that habitat-scale and bay-scale movement is species specific and varies both spatially and temporally for late juvenile red drum and spotted seatrout. At the habitat scale, seagrass was used extensively by both species, while red drum were also commonly associated with the oyster reef at Mud Island. Red drum occupied shallower areas of the seascape relative to spotted seatrout, and diel shifts in habitat use and movement rates were observed and possibly linked to diel shifts in foraging activity. At the bay-scale, red drum and spotted seatrout showed the capacity for directed movements of at least 70 km. Nevertheless, the majority of red drum and spotted seatrout were primarily detected within a few kilometers of their release site, suggesting that the population dynamics of both species is probably tied to local processes. Directed bay-scale movements made by small contingents of both species were seasonal, occurring during winter and early spring. In sum, habitat use and movement of red drum and spotted seatrout is influenced by seascape structure at both the habitat and bay scale. Moreover, conspicuous diel and seasonal shifts at both spatial scales indicate that the functional value of habitat types within the Mud Island seascape as well as larger areas associated with the MANERR can change over time.

The results of this study have important implications for the management of each species and the habitats they occupy. Habitat use patterns suggest that heterogeneous habitat assemblages including structured habitat should be prioritized for conservation and/or restoration. Seagrasses and oyster reef are frequently targeted for these efforts (Grabowski and Peterson 2007; Katwijk et al. 2009), and results suggest this should benefit late juvenile red drum and spotted seatrout, though depth of the affected habitat should be considered. Limited bay-scale movement and high residency suggest that estuary-specific management of late juvenile red drum and spotted seatrout is appropriate, especially if local conditions require mitigation. If necessary, designated reserves such as the MANERR may be conducive to specific management regulations such as reduced bag limits or no take zones. High residency also indicates that stock enhancement efforts for both species should be distributed throughout estuarine systems to ensure widespread impact. In conclusion, aiming management strategies at both the habitat and bay scale will help ensure the continued sustainability of late juvenile red drum and spotted seatrout populations.

REFERENCES

Adams, D. H., and D. M. Tremain. 2000. Association of large juvenile red drum, *Sciaenops ocellatus*, with an estuarine creek on the Atlantic coast of Florida. *Environmental Biology of Fishes* 58(2): 183-194.

Aebischer, N. J., P. A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74(5), 1313-1325.

Andrews, K. S., N. Tolimieri, G.D. Williams, J.F. Samhouri, C.J. Harvey, and P.S. Levin. 2011. Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. *Marine Biology* 158(10): 2377-2387.

Attrill, M. J., J.A. Strong, and A.A. Rowden. 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23: 114-121.

Bacheler, N. M., L. M. Paramore, S. M. Burdick, Buckel, and J. E. Hightower. 2009. Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. *Fishery Bulletin* 107(4): 405-418.

Baker, R., and M. Sheaves. 2007. Shallow-water refuge paradigm: conflicting evidence from tethering experiments in a tropical estuary. *Marine Ecology Progress Series* 349: 13-22.

Beck, M. W., K.L. Heck Jr, K. W. Able, D. L. Childers, D. B. Eggleston, B.M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and

M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51(8): 633-641.

Becker, A., and I.M. Suthers. 2014. Predator driven diel variation in abundance and behaviour of fish in deep and shallow habitats of an estuary. *Estuarine, Coastal and Shelf Science* 144: 82-88.

Bingham, R. L., L.A. Brennan, and B.M. Ballard. 2010. Discrepancies between Euclidean distance and compositional analyses of resource selection data with known parameters. *The Journal of Wildlife Management* 74(3): 582-587.

Boström, C., E. L. Jackson, and C.A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: a review. *Estuarine, Coastal and Shelf Science* 68(3): 383-403.

Boström C., S.J. Pittman, C. Simenstad, and R.T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series* 427: 191-217.

Callihan, J. L., J. H. Cowan Jr, and M. D. Harbison. 2014. Sex-specific movement response of an estuarine sciaenid (*Cynoscion nebulosus*) to freshets. *Estuaries and Coasts* 38(5): 1-13.

Capossela, K. M., M.C. Fabrizio, and R. W. Brill. 2013. Migratory and within-estuary behaviors of adult summer flounder (*Paralichthys dentatus*) in a lagoon system of the southern mid-Atlantic Bight. *Fishery Bulletin* 111(2): 189-201.

Childs, A. R., P.D. Cowley, T.F. Næsje, A. J. Booth, M. W. Potts, E. B. Thorstad and F. Økland. 2008. Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. *Estuarine, Coastal and Shelf Science* 78(1): 227-236.

Comyns, B. H., C.F. Rakocinski, M.S. Peterson, and A.M. Shiller. 2008. Otolith chemistry of juvenile spotted seatrout *Cynoscion nebulosus* reflects local natal regions of coastal Mississippi, USA. *Marine Ecology Progress Series* 371: 243-252.

Conner, L. M. and B.W. Plowman. 2001. Using Euclidean distances to assess nonrandom

habitat use. In *Radio Tracking and Animal Populations*. pp. 275–290. San Diego, CA: Academic Press.

Conner, L. M, M.D. Smith, and L.W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. *Ecology* 84(2): 526-531.

Dance, M.A., and J.R. Rooker. Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. In review. *Estuarine, Coastal and Shelf Science.*

Espinoza, M., T.J. Farrugia, D. M. Webber, F. Smith, and C. G. Lowe. 2011a. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research* 108(2): 364-371.

Espinoza, M., T.J. Farrugia, and C. G. Lowe. 2011b. Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. *Journal of Experimental Marine Biology and Ecology* 401(1): 63-74.

Facendola, J. J., and F.S. Scharf. 2012. Seasonal and ontogenetic variation in the diet and daily ration of estuarine red drum as derived from field-based estimates of gastric evacuation and consumption. *Marine and Coastal Fisheries* 4(1): 546-559.

Farrugia, T. J., M. Espinoza and C.G. Lowe. 2011. Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. *Marine and Freshwater Research* 62(6): 648-657.

Flaherty-Walia, K. E., R.E. Matheson Jr, and R. Paperno. 2015. Juvenile spotted seatrout (*Cynoscion nebulosus*) habitat use in an eastern Gulf of Mexico estuary: the effects of seagrass bed architecture, seagrass species composition, and varying degrees of freshwater influence. *Estuaries and Coasts* 38(1): 353-366.

Fodrie, F. J., L.A. Yeager, J. H. Grabowski, C.A. Layman, G.D. Sherwood and M.D. Kenworthy. 2015. Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization. *Oecologia* 178(1): 75-87.

Fraser, N. H. C., and N.B. Metcalfe. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology* 11(3): 385-391.

Furey, N. B., M.A. Dance, and J.R. Rooker. 2013. Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. *Journal of Fish Biology* 82(5): 1469-1483.

Gannon, D. P., and D.M. Waples. 2004. Diets of coastal bottlenose dolphins from the US mid-Atlantic coast differ by habitat. *Marine Mammal Science* 20(3) 527-545.

Gillanders, B.M. 2006. Seagrasses, fish, and fisheries. In *Seagrasses: Biology, Ecology, and Conservation*. Springer Netherlands. 503-505.

Gjelland, K. Ø., and R.D. Hedger. 2013. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution* 4(7): 665-674.

Grober-Dunsmore, R., S.J. Pittman, C. Caldow, M.S. Kendall, and T.K. Frazer. 2009. A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In *Ecological Connectivity Among Tropical Coastal Ecosystems*. Springer Netherlands. 493-530.

Heck Jr, K. L., and R.J. Orth. 2006. Predation in seagrass beds. In *Seagrasses: Biology, Ecology and Conservation*. Springer Netherlands. 537-550.

Heupel, M. R., J.M. Semmens, and A.J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* 57(1): 1-13.

Kennish, M. J. 2002. Environmental threats and environmental future of estuaries. *Environmental Conservation* 29(1): 78-107.

Kinney, M. J., N.E. Hussey, A.T. Fisk, A.J. Tobin, and C.A. Simpfendorfer. 2011. Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. *Marine Ecology Progress Series* 439: 263-276.

Knickle, D. C., and G.A. Rose. 2014. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and CN isotopes. *Environmental Biology of Fishes* 97(4): 343-355.

Lanier, J. M., and F.S. Scharf. 2007. Experimental investigation of spatial and temporal variation in estuarine growth of age-0 juvenile red drum (*Sciaenops ocellatus*). *Journal of Experimental Marine Biology and Ecology* 349(1): 131-141.

Llanso, R. J., S.S. Bell, and F.E. Vose. 1998. Food habits of red drum and spotted seatrout in a restored mangrove impoundment. *Estuaries* 21(2): 294-306.

MacRae, P. S., and J.H. Cowan Jr. 2010. Habitat preferences of spotted seatrout, *Cynoscion nebulosus*, in coastal Louisiana: a step towards informing spatial management in estuarine ecosystems. *The Open Fish Science Journal* 3: 154-163.

Main, K. L. 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. *Ecology* 68(1): 170-180.

McMichael, R. H., and K.M. Peters. 1989. Early life history of spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries* 12(2): 98-110.

Nagelkerken, I., M. Sheaves, R. Baker, and R.M. Connolly. 2014. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16(2): 362-371.

Neahr, T. A., G.W. Stunz, and T.J. Minello. 2010. Habitat use patterns of newly settled spotted seatrout in estuaries of the north-western Gulf of Mexico. *Fisheries Management and Ecology* 17(5): 404-413.

Nieland, D. L., R.G. Thomas, and C.A. Wilson. 2002. Age, growth, and reproduction of spotted seatrout in Barataria Bay, Louisiana. *Transactions of the American Fisheries Society* 131(2): 245-259.

Payne, L.M. 2011. Evaluation of large-scale movement patterns of spotted seatrout (*Cynoscion nebulosus*) using acoustic telemetry. Master's thesis. Texas A&M University-Corpus Christi, Corpus Christi, Texas.

Peters, K. M., and R.H. McMichael. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries* 10(2): 92-107.

Porch, C. E., C.A. Wilson, and D.L. Nieland. 2002. A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates. *Fishery Bulletin* 100(1): 149-152.

Rakocinski, C.F., D.M. Baltz, and J.W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* 80: 135-148.

Reebs, S. G. 2002. Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries* 12(4): 349-371.

Reese Robillard, M. M., L.M. Payne, R.R. Vega, and G.W. Stunz. 2015. Best practices for surgically implanting acoustic transmitters in spotted seatrout. *Transactions of the American Fisheries Society* 144(1): 81-88.

Rooker, J. R., and S.A. Holt. 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: patterns of distribution and growth. *Marine Ecology Progress Series* 158: 139-149.

Rooker, J. R., S.A. Holt, M.A. Soto, and G. J. Holt. 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21(2): 318-327.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 2: 352-388.

Scharf, F. S., and K.K. Schlicht. 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator-prey size relationships. *Estuaries* 23(1): 128-139.

Simpfendorfer, C. A., M.R. Heupel, and R.E. Hueter. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences* 59(1): 23-32.

Stunz, G. W., T.J. Minello, and P.S. Levin. 2002. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. *Marine Ecology Progress Series* 238: 227-236.

Stunz, G. W., T.J. Minello, and L.P. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Marine Ecology Progress Series* 406: 147-159.

Walsh, C. T., I.V. Reinfelds, M.C. Ives, C.A. Gray, R.J. West, and D.E. van der Meulen. 2013. Environmental influences on the spatial ecology and spawning behaviour of an estuarine-resident fish, *Macquaria colonorum*. *Estuarine, Coastal and Shelf Science* 118: 60-71.

Werner, E. E., D.J. Hall, D.R. Laughlin, D.J. Wagner, L.A. Wilsmann, and F.C. Funk. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Board of Canada* 34(3): 360-370.

Wilson, C. J., P.S. Wilson, C.A. Greene, and K.H. Dunton. 2013. Seagrass meadows provide an acoustic refuge for estuarine fish. *Marine Ecology Progress Series* 472: 117-127.

APPENDIX A

Table 3. Habitat-scale detection data for late juvenile red drum (RD) and spotted seatrout (SST) tagged and released at Mud Island (Aransas Bay, TX). Positions were estimated using two methods: VR2W positioning system (VPS) and hourly center of activity (COA). Tracking duration was calculated as the number of days between the first and last recorded detection. Residency was calculated as the number of days fish were detected at least twice within the study site. Revisits were calculated as the number of times fish returned to the study site after an absence > 24 hours.

Species	ID	TL	Detections	COA positions	VPS positions	Tracking duration	Residency	Revisits
RD	10798	319	679	36	-	24	22	2
RD	10799	364	46	12	-	9	9	0
RD	10800	335	53	7	-	23	22	1
RD	10801	328	4753	278	87	27	13	5
RD	10802	345	181	10	-	26	6	1
RD	10803	352	23	6	-	23	4	1
RD	10845	398	124	14	1	26	14	8
RD	10846	416	856	47	33	27	14	4
RD	10847	407	557	54	9	28	27	2
RD	10848	419	801	47	13	12	5	2
RD	10849	399	446	103	-	1	1	0
RD	10850	346	194	16	-	26	7	4
RD	10851	319	2728	133	12	10	4	1
RD	10852	434	636	66	15	24	7	3
SST	10795	277	101	22	-	26	4	2
SST	10796	308	158	38	-	26	17	8
SST	10797	240	2753	184	135	27	26	1
SST	10835	257	34	7	-	21	2	1
SST	10836	268	77	16	-	22	7	3
SST	10837	254	77	17	-	23	6	3
SST	10838	276	604	58	-	27	9	2
SST	10839	308	511	52	24	28	18	10
SST	10840	244	7719	488	355	28	28	0
SST	10841	260	12345	575	532	28	28	0
SST	10842	271	4141	314	126	27	24	1
SST	10843	273	6156	407	198	28	27	1
SST	10844	301	146	13	-	2	2	0
SST	10853	269	30	5	-	14	2	1
SST	10854	273	7	1	-	1	1	0

APPENDIX B

Table 4. Bay-scale tracking data for all red drum (RD) and spotted seatrout (SST) individuals. Total length (TL) was measured and individuals were assigned an age class based on estimated age at the end of the calendar year in which they were tagged. Detections from the habitat-scale tracking array were not included in totals. Tracking duration was calculated as the time elapsed between release and the last recorded fish position (days). Distance traveled was calculated as the sum of minimum through-water distances (km) between fish positions, and final displacement was calculated as the minimum through-water distance (km) between release location and last recorded fish position.

Species	TL	ID	Release date	Age class	Detections	Tracking duration	Distance traveled	Final displacement
RD	398	10845	6/11/2013	2	321	202.3	0	0
RD	416	10846	6/11/2013	2	2218	451.7	9.8	0
RD	407	10847	6/11/2013	2	728	202.4	0	0
RD	419	10848	6/11/2013	2	443	498.5	0	0
RD	399	10849	6/12/2013	2	1216	204.5	0	0
RD	346	10850	6/12/2013	2	235	160.9	0	0
RD	319	10851	6/12/2013	2	39	232.8	10.0	4.9
RD	434	10852	6/12/2013	2	605	348.4	10.3	1.5
RD	319	10798	6/13/2013	2	27	248.6	0	0
RD	364	10799	6/13/2013	2	1187	229.4	0	0
RD	335	10800	6/14/2013	2	222	495.8	0	0
RD	328	10801	6/14/2013	2	17087	339.6	0	0
RD	345	10802	6/14/2013	2	96	164	0	0
RD	352	10803	6/15/2013	2	530	498.3	0	0
RD	396	10804	7/22/2013	2	110	209.6	69.6	6.3
RD	428	10805	7/22/2013	2				
RD	400	10806	7/22/2013	2	5	210.7	33.0	8.2
RD	385	10807	7/22/2013	2				
RD	399	10808	7/22/2013	2	5	154.1	5.2	3.2
RD	400	10809	7/22/2013	2				
RD	234	10810	7/22/2013	1	11	147.2	3.2	3.2
RD	404	10811	7/22/2013	2	6061	310.5	0	0
RD	318	10812	7/22/2013	2	1013	245.6	0	0
RD	371	10813	7/22/2013	2	103	259.1	0	0
RD	252	10814	7/22/2013	1	544	3.3	0	0
RD	402	11792	7/23/2013	2	18	202.4	1.6	1.6
RD	390	11793	7/23/2013	2	20	44.8	6.8	6.8

RD	232	11794	7/23/2013	1	23	177.3	57.3	31.5
RD	241	11795	7/23/2013	1				
RD	251	11796	7/23/2013	1				
RD	223	11797	7/23/2013	1				
RD	240	11798	7/23/2013	1	23	161.3	8.6	0.6
RD	230	11799	7/24/2013	1				
RD	254	11800	7/24/2013	1				
RD	435	12993	11/20/2013	2	209	88.6	44.1	1.6
RD	485	12994	11/20/2013	2	20	44.4	1.6	1.6
RD	446	12995	11/20/2013	2	21	43.5	15.7	1.6
RD	329	12996	11/20/2013	1	220	522.7	18.7	0
RD	328	12997	11/21/2013	1	16446	273	0	0
RD	356	12998	11/21/2013	1	6100	272.9	0	0
RD	337	12999	11/21/2013	1	25	364.3	0.9	3.9
RD	451	13000	11/21/2013	2	337	265.6	0.9	0.9
RD	330	13001	11/21/2013	1	2204	487.7	16.4	2.3
RD	342	13002	11/21/2013	1	193	55.2	4.7	0
RD	537	13003	12/3/2013	2	8	55.3	12.0	2.2
RD	535	13004	12/3/2013	2	22	475.8	2.2	2.2
RD	497	13005	12/3/2013	2	65	364.8	20.7	2.2
RD	500	13006	12/3/2013	2	11	11.8	10.9	4.4
RD	496	13007	12/3/2013	2	3	54.7	6.8	6.8
RD	486	13008	12/3/2013	2				
RD	325	13009	12/4/2013	1	21	41.6	44.9	6.3
RD	351	13010	12/4/2013	1	50	448.1	27.1	13.3
RD	322	13011	12/4/2013	1	297	421	72.4	13.3
RD	333	13012	12/4/2013	1	47	174.8	9.4	0.5
SST	257	10835	6/11/2013	1	44	165.3	0	0
SST	268	10836	6/11/2013	1	190	240.3	68.6	11.1
SST	254	10837	6/11/2013	1	121	183.3	6.3	0
SST	276	10838	6/11/2013	1	604	26	0	0
SST	308	10839	6/11/2013	1	511	26.8	0	0
SST	244	10840	6/11/2013	1	8090	262.9	56.9	0
SST	260	10841	6/11/2013	1	13134	206.5	29.6	4.9
SST	271	10842	6/11/2013	1	4189	38.7	0	0
SST	273	10843	6/11/2013	1	6898	240.9	0	0
SST	301	10844	6/11/2013	1	146	0.6	0	0
SST	277	10795	6/12/2013	1	996	267.3	36.8	0
SST	308	10796	6/12/2013	1	303	233.3	1.5	0

SST	269	10853	6/12/2013	1	30	13	0	0
SST	273	10854	6/12/2013	1	7	0.02	0	0
SST	240	10797	6/12/2013	1	2771	91.8	4.9	4.9