Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery

CrossMark

Michael A. Dance [a, b, *], Jay R. Rooker [a, b]

[a] Department of Marine Biology, Texas A&M University, 1001 Texas Clipper Rd., Galveston, TX 77554, USA
[b] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77840, USA

ABSTRACT

Acoustic telemetry was used to examine habitat- and bay-scale connectivity for co-occurring juvenile fishes, southern flounder (*Paralichthys lethostigma*) and red drum (*Sciaenops ocellatus*), at two spatial scales in a model estuarine seascape. An acoustic positioning system was deployed to examine habitat-scale (ca. 1 m—1 km) movement, while a larger gridded array was deployed to examine bay-scale movement (ca. 1—20 km). Both species exhibited greater use of edge habitat and seagrass beds at the habitat scale; however, rates of movement within habitats varied between species. Southern flounder movement (mean = 4.0 m min^{-1}) increased with decreasing habitat complexity (seagrass to bare sand) and increasing temperature, while red drum rate of movement (mean = 8.4 m min^{-1}) was not significantly affected by environmental factors at the habitat scale, indicating the use of different foraging strategies (i.e. ambush vs. active). Bay-scale distribution was influenced by physicochemical conditions and seascape composition, with both species found most frequently in areas with high seagrass coverage and relative close proximity to tidal creeks and connective channels. Response to environmental variables often differed between species and the probability of bay-scale movement (>1 km) for southern flounder was greatest on days with narrow tidal ranges (<0.4 m) and higher temperatures (>17 °C), while the probability of bay-scale movement for red drum increased in response to decreasing salinity and lower temperatures (<16 °C). Species-specific variation in movement patterns within and across habitat types observed here at both the habitat and bay scale suggest sympatric species employ different strategies to partition resources within estuarine nursery areas and highlight the importance of multi-species assessments for improving our understanding of habitat value and ecosystem function.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Estuarine and coastal ecosystems are highly productive areas that provide a range of ecosystem services and are critical to maintaining valuable marine fisheries (Worm et al., 2006; Barbier et al., 2011). For fishes and invertebrates that utilize both estuarine and coastal areas to complete their life cycle, habitats such as seagrasses, salt marsh, mangroves, and oyster reefs often serve as nurseries (Beck et al., 2001; Dahlgren et al., 2006). Unfortunately, many of these habitats are in global decline due to anthropogenic stressors (Waycott et al., 2009; Beck et al., 2011; Barbier et al., 2011).

This has led to an increased focus on refining the nursery concept, and quantifying the relative contribution (i.e. value) of estuarine nursery habitats to adult populations (Dahlgren et al., 2006; Vasconcellos et al., 2011). However, marine organisms often use multiple habitats within an estuary during adolescence, and connectivity between habitat types remains poorly understood for many species (Boström et al., 2011), complicating our interpretation of species—habitat relationships. Thus, an improved understanding of habitat linkages and environmental processes governing spatial distributions of estuarine taxa within a seascape is needed to develop efficacious ecosystem-based management plans (Nagelkerken et al., 2015, Sheaves et al., 2015).

Estuarine seascapes are comprised of a complex mosaic of different habitat types, and the spatial configuration of habitats (e.g. size, shape, proximity to other habitats) may juxtapose complementary resources (e.g. shelter, foraging opportunities, movement corridors), influencing fitness and/or survival of resident

* Corresponding author. Department of Marine Biology, Texas A&M University, 1001 Texas Clipper Rd., Galveston, TX 77554, USA.
E-mail addresses: dancema@tamu.edu (M.A. Dance), rookerj@tamug.edu (J.R. Rooker).

species (Grober-Dunsmore et al., 2009). As juvenile fishes become more mobile during ontogeny, individuals are increasingly capable of utilizing multiple habitats (Gillanders et al., 2003), and movement patterns between habitat types and patches can provide important information on environmental and behavioral processes driving habitat use and habitat connectivity (Grober-Dunsmore et al., 2007). Still, the fact that movement patterns can be interpreted at a range of spatial scales and may vary seasonally or between co-occurring taxa, complicates efforts to identify and conserve critical nurseries (Dorenbosch et al., 2007; Boström et al., 2011).

The advent of acoustic telemetry has enabled researchers to monitor continuous movement patterns of fish in estuarine seascapes (Cooke et al., 2004). However, the interpretation of fish-habitat (i.e., spatial) relationships from acoustic telemetry studies is often limited because passive telemetry data typically lack the positional accuracy needed to assess habitat-scale movements (Heupel et al., 2006). Recently, high-density arrays of passive receivers with overlapping detection radii have been used to triangulate fish positions at resolutions comparable to active tracking, providing fine-scale information on habitat use and movement (Espinoza et al., 2011). Acoustic positioning arrays such as Vemco's VR2W Positioning System (VPS) and Lotek's Asynchronous Logger Positioning System (ALPS) have been used successfully to generate precise position estimates in a variety of estuarine settings, and represent promising technologies for improving our understanding of fish–habitat relationships within estuarine seascapes (Espinoza et al., 2011; Grothues et al., 2012; Furey et al., 2013).

Here we use acoustic telemetry to examine habitat use and connectivity at two spatial scales (habitat, bay) for sympatric estuarine-dependent species: southern flounder (*Paralichthys lethostigma*) and red drum (*Sciaenops ocellatus*). Although both species co-occur in estuarine seascapes, southern flounder and red drum display contrasting foraging strategies (ambush vs. active predator), and therefore habitat associations and linkages within the estuary may differ. The importance of estuarine habitats (e.g. seagrasses, salt marsh) to newly settled individuals has been evaluated for both species (Rooker and Holt, 1997; Nanez-James et al., 2009; Furey and Rooker, 2013); however, our understanding of habitat requirements and factors influencing movement patterns for older, more mobile juveniles (age-1 to age-2) is limited. Because juveniles remain in estuarine seascapes for multiple years before joining coastal populations to spawn (Stunz et al., 2000; Powers, 2012), an improved understanding of estuarine habitat use and connectivity during the first few years of life is needed to develop management strategies that conserve habitats and seascapes that are essential to the life cycles of both species. The aim of this study was to characterize both habitat-scale (<1 km) and bay-scale (>1 km) patterns of habitat use for juvenile southern flounder and red drum and to identify environmental factors influencing movement and habitat selection of both species. Our working hypothesis is that an ambush predator (southern flounder) will demonstrate less movement than an active predator (red drum) and that habitat utilization (e.g. habitat associations and linkages) will differ between the two species. In addition, because areas at the interface of two or more habitat types (i.e. edges) are known to be important foraging areas of predators (Boström et al., 2006), we hypothesize that despite potential differences in habitat utilization, both southern flounder and red drum will prefer complex seascapes with greater edge habitat.

2. Methods

The study was conducted in Christmas Bay, which is a small (~26 km^2) sub-bay located at the southwestern extreme of the greater Galveston Bay Estuary (GBE) in the northwestern Gulf of Mexico (Fig. 1). Christmas Bay is utilized by both species (Furey et al., 2013; Stunz et al., 2002) and contains representative habitats found throughout the GBE (salt marsh, oyster reef, non-vegetated substrate). It is distinct ecologically from other locations within the GBE because it contains the last significant natural stands of seagrass, with both shoal grass *Halodule wrightii* and turtle grass *Thalassia testudinum* well represented (Adair et al., 1994). Christmas Bay is surrounded by intertidal salt marsh (smooth cordgrass, *Spartina alterniflora*), with non-vegetated substrate and oyster reef often found in close proximity to or interspersed within seagrass beds and adjacent to the intertidal marsh. Deeper subtidal channels connect Christmas Bay to surrounding bays in the GBE as well as the Gulf of Mexico via San Luis Pass (one of two inlets connecting the GBE to the Gulf of Mexico), providing potential movement corridors for inter-bay and estuarine-coastal connectivity (Fig. 1B). Because fish within Christmas Bay have access to multiple habitat types in close proximity as well as neighboring bays within a modest spatial extent, this Bay was chosen to examine estuarine habitat use and movement of juvenile southern flounder and red drum.

Acoustic telemetry arrays were deployed at two spatial scales in Christmas Bay: 1) habitat scale and 2) bay scale. For the purposes of this study, habitat scale refers to movement and habitat use within a seascape (defined as 1 m–1 km) and bay scale refers to movement and habitat use among multiple seascapes in an estuary (1–20 km). A Vemco VR2W Positioning System (VPS) was deployed to examine habitat-scale patterns of use and movement (Fig. 1C). VPS utilizes an array of closely spaced receivers with overlapping detection ranges to triangulate fish positions based on differences in time of arrival to three or more receivers and has a potential accuracy of about 1–3 m (Espinoza et al., 2011; Furey et al., 2013). The VPS deployed in Christmas Bay consisted of 10 closely spaced (~50 m) VR2W omnidirectional acoustic receivers along the southern shoreline in an area with all major habitat types represented (Fig. 1C). Synchronizing transmitters or "sync tags" (Vemco V9-1H, 69 kHz) with a nominal delay of 600 s (range: 500–700 s) were deployed within the VPS to synchronize the internal clocks of the VPS receivers and act as reference tags. To examine bay-scale habitat use and movement, a larger gridded array (~1 km spacing) of VR2W receivers (n = 13) was initially deployed throughout Christmas Bay in January 2012 (Fig. 1B). After completion of the VPS portion of the study, nine receivers from the VPS (one was left in place at the VPS location) were added to the bay-scale array and relocated to exit points, connective sub-tidal channels, and surrounding bays in February 2012 to expand our spatial coverage (Fig. 1).

Benthic habitats (channel, oyster, salt marsh, sand, seagrass, tidal creek) were characterized and mapped at two spatial resolutions in ArcGIS 10.0: 1) habitat scale and 2) bay scale. Orthorectified satellite imagery was used to classify boundaries or edges of salt marsh, turtle grass, and oyster reefs within the habitat-scale array. *In situ* observations at 235 point locations (approximately half in a gridded arrangement and half strategically placed along habitat boundaries) throughout the VPS area were then used to verify habitat classifications and boundaries (Furey et al., 2013). After verification was completed, habitats were digitized in ArcGIS 10.0 for analysis purposes. At the bay scale, salt marsh edge was defined as the interface of open water and intertidal emergent salt marsh vegetation from georeferenced National Wetlands Inventory maps (Cowardin et al., 1979). Intertidal creek entrances (hereafter referred to as "tidal creeks") linking open water to the salt marsh were identified from orthorectified satellite images taken on January 11, 2012 (0.3 m resolution, U.S. Geological Survey). Subtidal channels connecting Christmas Bay to surrounding bays
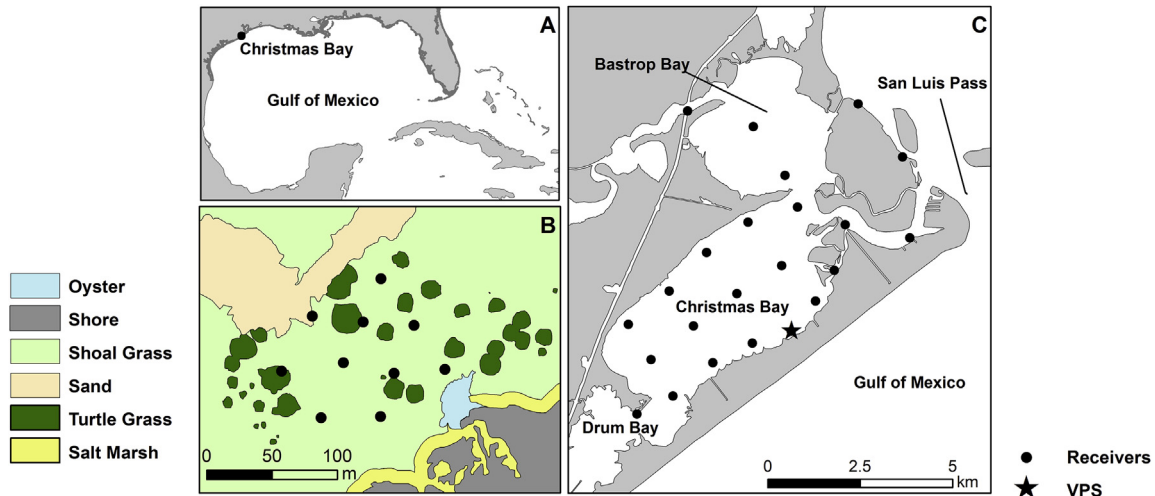
Fig. 1. Map of study site. A) Location of Christmas Bay, Texas. B) Layout of Christmas Bay and surrounding sub-bays with location of the habitat-scale array and bay-scale acoustic telemetry array. C) Layout of VPS acoustic telemetry array and spatial arrangement of habitats within the array.

were collectively grouped as channel habitat. Seagrass and oyster coverage data layers were obtained from the National Oceanic Atmospheric Administration National Coastal Data Development Center (NOAA NCDDC). Bathymetry data were obtained from digital elevation models of the GBE created from NOAA hydrographic sounding surveys (Taylor et al., 2008).

Environmental conditions within Christmas Bay and associated channels were monitored for the duration of the study. Temperature data loggers (Onset Inc.) were co-located with a subset of receivers and used to record water temperature every 15 min in the habitat-scale array (n = 6) and every 30 min at the bay scale (n = 13). For each individual fish location, water temperature was determined as the recorded temperature from the nearest data logger at the approximate time stamp of the fish location. High and low tide predictions for Christmas Bay (NOAA, 2012) were used to determine daily tidal range within the study area. Barometric pressure, wind velocity, and wind direction (6 min intervals) were obtained from National Data Buoy Center (NDBC) Buoy 8772447 located 15 km southwest of Christmas Bay. Because salinity measurements within Christmas Bay were limited to measurements taken on 5 different days during the study, daily salinity readings acquired from Galveston Bay (NDBC Buoy 8771013) were used to estimate daily salinity. Salinity measurements taken in Christmas Bay during the study period were regressed against corresponding daily salinity values obtained from Galveston Bay. The resulting linear equation was then used to convert known daily salinity from Galveston Bay to an approximate daily salinity for Christmas Bay.

Juvenile (age 1—2) southern flounder (n = 8) and red drum (n = 14) were captured via hook and line in Christmas Bay and externally fitted with coded transmitters (Vemco V9-1H, 69 kHz) with a nominal code transmission delay of 120 s (range: 60—180 s). Prior to tagging, individuals were kept in 0.7 m^3 tanks at the Texas A&M University Wetlands Center. Fish were anaesthetized with clove oil and tagged following a protocol described by Furey et al. (2013) in which each transmitter is placed in a latex sleeve that is externally mounted to the dorsal musculature of the fish. Two sterilized nickel pins (held in place by a vinyl Peterson disc tag; Floy Tag Inc.) were passed through the dorsal musculature and secured to the latex sleeve with rubber earring backings and a metal crimping sleeve. Tagged individuals were then monitored for a minimum of 24 h to ensure full recovery from the tagging procedure before release. All tagged southern flounder and red drum

were released into the habitat-scale array on January 15, 2012 and tracked for 30 days with the VPS and until May 1, 2012 in the bay-scale array.

2.1. Data analyses

Prior to analysis, data from the habitat-scale array were filtered by horizontal position error (HPE), a relative, dimensionless measure of error sensitivity calculated by the VPS (Espinoza et al., 2011). For this study, only positions with an HPE <12 were included in the analysis, after in situ analysis of 4 static V9-H transmitters within the array indicated positioning error was generally <2 m (1.61 ± 0.01 m, mean ± SE) for calculated positions with an HPE < 12. While previous studies have reported that including VPS positions with HPE values equal to or less than 15 are acceptable (Espinoza et al., 2011), we chose a more conservative approach because some habitat patches in Christmas Bay are relatively small (<5 m diameter). VPS positions within the first 30 min were also omitted from habitat-scale analysis to minimize the influence of release location on fish positions. Likewise, detections within the first 6 h were removed from bay-scale analyses to allow fish time to disperse from the release location. Because only three fish were detected after March 31, 2012, bay-scale analyses of habitat use and movement were restricted to detections from the first 77 days of the study.

Habitat-scale connectivity within the VPS area was analyzed using Euclidean distance-based analysis (EDA; Conner et al., 2003), which uses distance to habitat rather than the proportion of positions within a habitat. This approach has been previously used in acoustic telemetry studies to describe habitat use within areas with multiple habitat types (Mason and Lowe, 2010; Furey et al., 2013). Because EDA is a distance-based approach, it minimizes habitat misclassification due to positioning error while also identifying the importance of edge habitats (interface of two or more habitats) and the influence of multiple habitats on an animal's position (Conner et al., 2003). EDA ratios were estimated by first generating 1000 random points within the habitat-scale array, defined here as the area within 120 m from at least three receivers (a conservative estimate of the area in which the VPS could reliably estimate a fish position with an HPE < 12). EDA ratios were then calculated for each unique individual—habitat combination by dividing the mean distance of an individual's VPS positions to a habitat type (oyster, salt marsh, sand, shoal grass, or turtle grass) by the mean distance

of random points to the respective habitat type. In addition to available habitat types, EDA ratios were also calculated for edge habitat, based on the distance from a point to the nearest boundary between two habitats. EDA is expressed as a ratio, and equal to 1 when habitat use is random (mean animal distance to habitat = mean distance of random points to habitat); EDA ratios that differ significantly from 1 indicate an individual was found relatively closer to (<1) or farther from (>1) a particular habitat than would be expected. Because each individual has a unique EDA ratio for each habitat type, the individual was retained as the experimental unit. Multivariate analysis of variance (MANOVA) was used to test for non-random habitat use for each species by determining if EDA ratios differed significantly from 1. If overall habitat use was found to be non-random, analysis of variance (ANOVA) was performed to determine which habitat types were used more or less than expected.

Rate of movement within the habitat-scale array was calculated as the distance traveled between two successive positions divided by the elapsed time. To reduce the possibility of underestimating rates of movement due to missing detections, mean rates of movement were only calculated using steps where the elapsed time between positions was less than 10 min. ANOVA was used to test for differences in mean rate of movement among different habitats and between species. Mean rate of movement was calculated for 1 °C temperature bins ranging from 12 to 22 °C and fit with a linear regression to examine the effects of temperature on the movement of each species.

Hierarchical cluster analysis and multidimensional scaling techniques (PRIMER 6, Clarke and Gorley, 2006) were used to examine fish–habitat relationships at the bay scale of both species. Habitat characteristics based on areal coverage (seagrass coverage, oyster coverage, total marsh edge) and distances to a habitat feature (distance to nearest tidal creek or channel) were calculated for the listening area of each receiver (defined as a 300 m radius, based on mean detection probability of 0.8 or greater in range testing) in the bay-scale array. A Bray–Curtis pairwise similarity matrix was calculated from the resulting multivariate receiver-habitat data. Hierarchical clustering and non-metric multidimensional scaling (nMDS) were then applied to the similarity matrix and used to separate receivers from the bay-scale array into natural groupings based on similarities (70%) in habitat composition. ANOVA was then used to test for differences in habitat use between species and across habitat groupings within species, by comparing the mean proportion of detections at receivers within each habitat grouping. Mean 50% and 95% kernel density plots were calculated for each species using the Spatial Analyst toolbox in ArcGIS 10.0 to help visualize the spatial distribution of tagged juvenile southern flounder and red drum within Christmas Bay. Kernels were generated from mean daily positions of individual fish, calculated using the center of activity (COA) algorithm described by Simpfendorfer et al. (2002).

Mixed effects generalized additive models (GAMs), using individual fish as a random factor, were used to examine the effects of environmental conditions on daily movement of southern flounder and red drum at the bay scale. To determine the influence of environmental factors on the probability of bay-scale movement (~1 km based on receiver spacing), daily movement within the bay-scale array (0 = non-movement, 1 = movement) was modeled against daily environmental factors [precipitation, salinity (mean), salinity variation, temperature (mean), wind direction (mean), temperature variation, tidal range, variation in barometric pressure, and variation in wind speed]. Temperature variation and variation in barometric pressure were calculated as the difference between maximum and minimum measurements for a particular day. Because salinity was only available as a daily mean, variation in

salinity was calculated as the difference in salinity between two successive days. Binomial GAMs with a logit link were then fit with cubic regression splines within the mgcv library (Wood, 2006, 2008) using R software (R Core Team, 2014). Cubic splines were restricted to 3 degrees of freedom to prevent overfitting (Rooker et al., 2012). Final models were selected using a manual backwards selection procedure based on minimizing Akaike information criterion (AIC) (Akaike, 1974). After selection of a final model for each species, each explanatory variable was excluded from the final model and the change in percent deviance explained (ΔDE) and AIC (ΔAIC) was compared to help determine the relative importance of each variable to the final model (Rooker et al., 2012; Furey et al., 2013). Total distance traveled within the array was calculated by taking the cumulative sum of distances between daily mean positions calculated using the COA algorithm (Simpfendorfer et al., 2002).

3. Results

A total of 9,214 fish positions were estimated by the VPS (from 90,485 detections) and 87,286 fish detections were recorded by the bay-scale array, of which 6,813 (74%) and 85,650 (95%) were retained, respectively, after data filtering (for HPE and time constraints). For southern flounder, 77% (6,234) of VPS positions and 95% (18,094) of bay scale detections were retained, while 54% of VPS positions (579) and 99% of bay-scale detections were retained for red drum (67,556). No VPS positions were retained for two red drum (ID: 3661, 3663) after data filtering; therefore, these individuals were not used in EDA analysis at the habitat scale (Table 1).

Habitat use within the habitat-scale array was found to be non-random for both red drum and southern flounder (MANOVA; $p < 0.01$). Univariate tests indicated that the proximity of red drum to turtle grass (mean EDA: 0.49, ANOVA; $p < 0.05$) and sand habitats (EDA: 0.44, ANOVA; $p < 0.05$) was significantly closer than expected. In contrast, proximity to oyster, salt marsh, and shoal grass was found to be random (EDA: 0.73 to 1.11, ANOVA; $p > 0.05$) (Fig. 2). Southern flounder habitat use was also non-random with individuals detected significantly closer to turtle grass (EDA: 0.31, ANOVA; $p < 0.05$) and oyster (EDA: 0.63, ANOVA; $p < 0.05$) than expected. Proximity to salt marsh, shoal grass, and sand habitats did not differ from random (EDA: 0.75 to 1.0, ANOVA; $p > 0.05$) (Fig. 2). Both species were found more closely associated with edge habitat than expected (EDA: 0.53 and 0.40 for red drum and southern flounder, respectively, ANOVA; $p < 0.01$).

The effects of temperature and habitat type on habitat-scale movement were assessed for both species by examining rates of movement within the habitat-scale array. Mean rates of movement were significantly greater for red drum (8.4 ± 0.5 m min^{-1}; mean ± SE) than southern flounder (4.0 ± 0.1 m min^{-1}) at the habitat scale (ANOVA; $p < 0.01$). Movement differed among habitat types for southern flounder (ANOVA; $p < 0.01$), with significantly reduced rates of movement observed from turtle grass (1.4 ± 0.1 m min^{-1}) relative to both sand (6.9 ± 0.2 m min^{-1}) and shoal grass habitats (3.0 ± 0.1 m min^{-1}) (Tukey's HSD; $p < 0.01$; all comparisons) (Fig. 3). Mean rate of movement among habitat types was not significantly different for red drum (ANOVA; $p > 0.05$). A significant positive relationship was also detected between temperature and rate of movement for southern flounder, increasing at a rate of 1.1 m min^{-1} per 1 °C (regression; $p < 0.01$) (Fig. 4). Temperature did not have a significant effect on the rate of movement by red drum (regression; $p > 0.05$).

Hierarchical clustering and two dimensional nMDS ordination plots identified three distinct habitat groupings at the bay scale, based on 70% similarity in multivariate seascape structure among
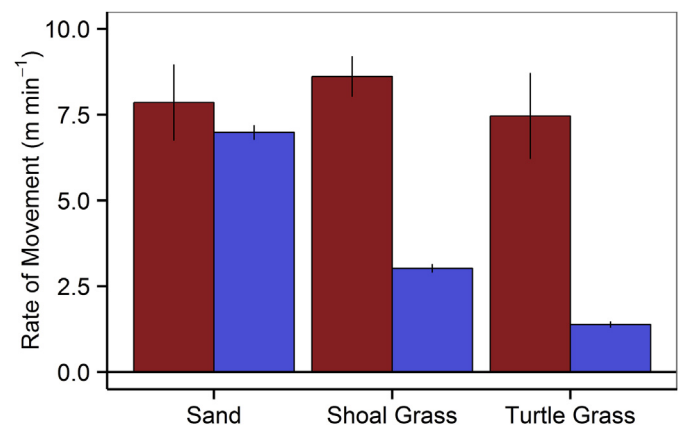
Table 1
Summary data for juvenile southern flounder (SF) and red drum (RD) tagged and released on January 15, 2012 and tracked through May 1, 2012 in Christmas Bay, Texas. Duration detected was calculated for as the number of days between the first detection and last detection. Total distance tracked is the cumulative linear distance between daily mean point locations, calculated as the daily center of activity (COA), based on the algorithm described by Simpfendorfer et al. (2002). Max daily distance is the maximum observed distance traveled by each fish in a single day.

Species	ID	SL (mm)	Duration detected (days)	Total distance tracked (km)	Max daily distance (km)	VPS positions
SF	3655	215	41	6.83	2.08	370
SF	3664	228	41	8.55	1.05	537
SF	3665	223	62	11.38	3.21	233
SF	3666	224	70	9.94	2.21	1433
SF	3667	237	62	12.62	0.83	762
SF	3668	219	107	6.95	0.00	3816
SF	3675	280	19	3.85	1.05	633
SF	3676	295	18	3.66	0.23	354
RD	3656	280	31	5.65	3.28	14
RD	3657	280	4	2.37	1.05	18
RD	3658	285	5	6.15	4.83	44
RD	3659	290	57	63.51	7.33	55
RD	3660	278	36	4.38	3.05	34
RD	3661	287	108	2.03	1.05	5
RD	3662	285	31	11.70	5.64	12
RD	3663	287	17	24.68	7.69	8
RD	3669	417	12	4.56	3.23	12
RD	3670	400	48	3.56	1.20	9
RD	3671	440	50	34.61	4.19	789
RD	3672	430	5	2.37	1.32	23
RD	3673	415	108	2.03	1.04	21
RD	3674	413	34	5.61	3.26	32
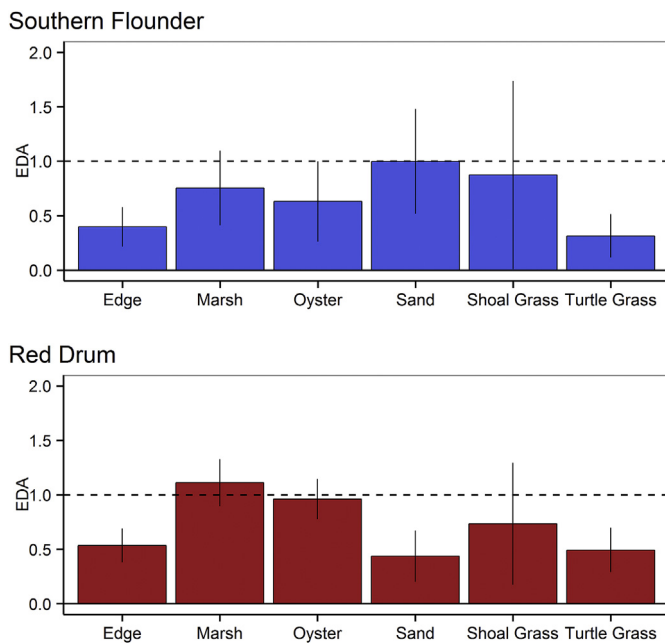
Fig. 2. Mean EDA ratios demonstrating fine-scale habitat use for southern flounder and red drum. EDA ratios = 1 indicate habitat use is random, EDA ratios <1 indicate relative preference, and EDA ratios >1 indicate relative avoidance. Error bars are ±1 standard deviation of the mean.

Fig. 3. Habitat-scale rates of movement (m min^{-1}) for southern flounder (blue) and red drum (red) across different estuarine habitat types. Habitat types include sand, shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*). Error bars represent ±1 standard error of the mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

acoustic receiver listening areas (Fig. 5). Listening areas for receivers in the first group were in or near subtidal channels with high marsh edge (HME), and close proximity to tidal creeks (Fig. 6). Listening areas for receivers in the second group were characterized by high seagrass coverage, intermediate marsh edge (IME), and moderate proximity to tidal creeks, while listening areas for receivers in the third group were characterized by non-vegetated bottom, no or low marsh edge (LME), and relatively high oyster coverage (far from tidal creeks and subtidal channels). The three natural 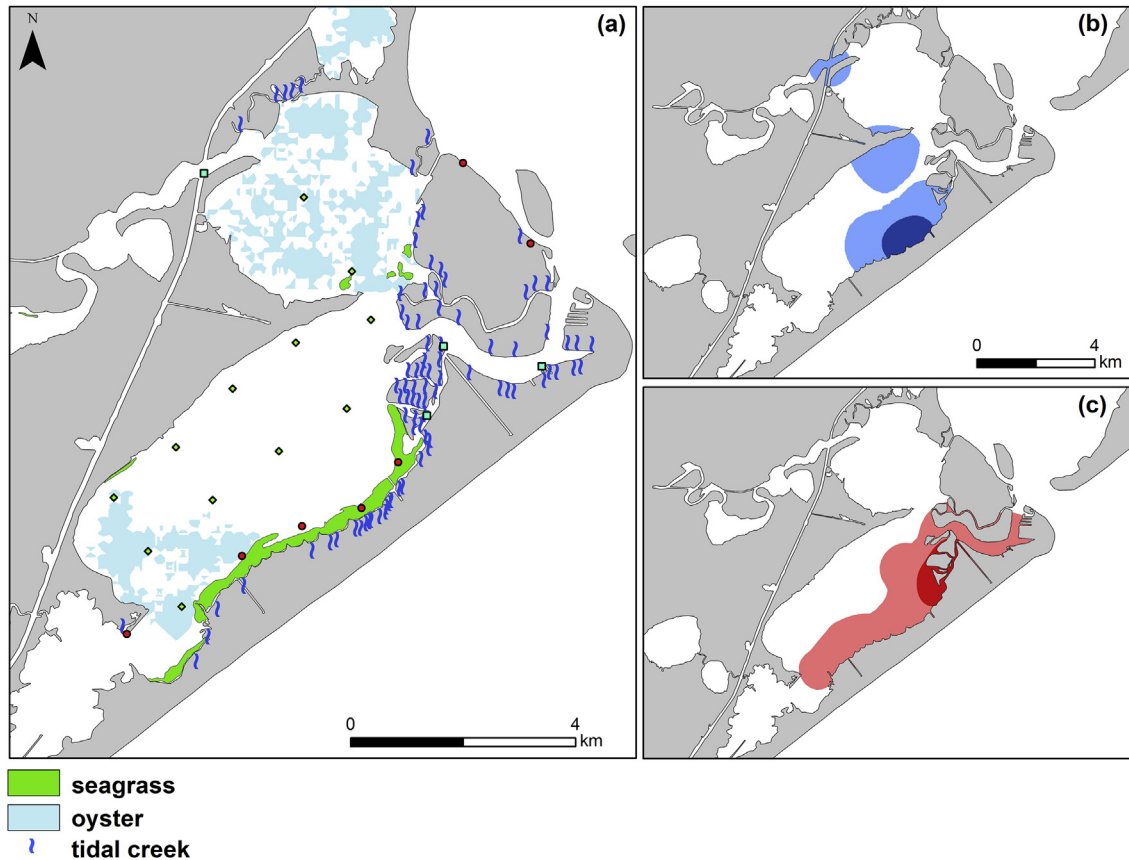groupings of receiver listening areas are hereafter referred to HME, IME, and LME seascapes. Significant differences in habitat use were apparent within species among habitat groups as well as between species within habitat groups (ANOVA; $p < 0.05$). Southern flounder were detected most frequently in IME seascapes (mean proportion of detections = 0.74), while also utilizing LME seascapes (0.20) more than HME (0.06) (Tukey's HSD; $p < 0.05$). Red drum were detected more frequently at IME relative to LME (mean proportion 0.57 and 0.10, respectively; Tukey's HSD; $p < 0.01$); however, proportional use of either of these areas did not differ significantly from HME seascapes (mean proportion 0.33; Tukey's HSD; $p > 0.05$) (Fig. 7). Species-specific comparisons revealed red drum exhibited greater use of HME seascapes (Tukey's HSD; $p < 0.05$), while no species-specific differences were found between IME and LME seascapes (Tukey's HSD; $p > 0.05$).

Total distance tracked within the bay-scale array ranged from 3.7 to 12.6 km (8.0 ± 1.2 km; mean ± SE) for southern flounder and from 2.0 to 63.5 km (12.4 ± 4.7 km) for red drum. Maximum daily
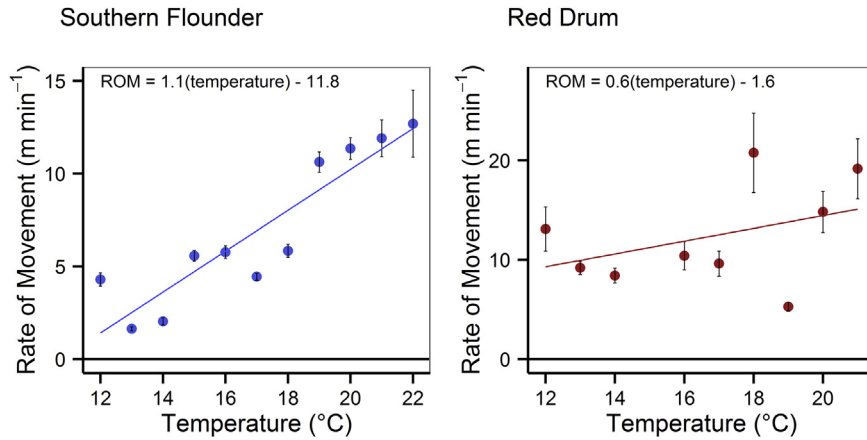
Fig. 4. Linear regressions of mean rate of movement (ROM) at the habitat scale against temperature for southern flounder (left, $r^2 = 0.83$) and red drum (right, $r^2 = 0.16$). Data points were derived from the species-specific mean rate of movement for $1°$ temperature bins. Error bars represent ± 1 SE of the mean.


seagrass
oyster
tidal creek

Fig. 5. Maps of Christmas Bay showing: bay-scale array with habitat coverage and acoustic receiver placement (a). Receiver groupings, based on 70% similarity in multivariate seascape structure among the receiver listening areas, were defined as high marsh edge (blue square), intermediate marsh edge (red circle), and low marsh edge (green diamond) seascapes. Panels (b) and (c) represent mean 50% (dark) and 95% (light) kernel distributions of southern flounder (b) and red drum (c). Kernels were derived from hourly center of activity points calculated using the methodology of Simpfendorfer et al. (2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

movement in one day was 3.2 km for southern flounder (1.2 ± 0.4 km; mean ± SE) and 7.7 km for red drum (3.4 ± 0.6 km). Final GAMs indicated that 5 environmental variables (salinity, salinity variation, temperature, tidal range, and variation in barometric pressure) influenced the probability of bay-scale movement (~1 km) for red drum and southern flounder, with temperature the only variable common between species-specific models. The final

GAM for bay-scale movement of southern flounder included the explanatory variables temperature, tidal range, and variation in barometric pressure with a percent deviance explained of 26.2% (AIC = 178.3). Model results indicated that daily tidal range was the most influential variable on southern flounder movement (Δ DE 8.1%, Δ AIC 16.0), with fish more likely to make bay-scale movements on days with little tidal variation (<0.4 m) (Fig. 8). Bay-scale
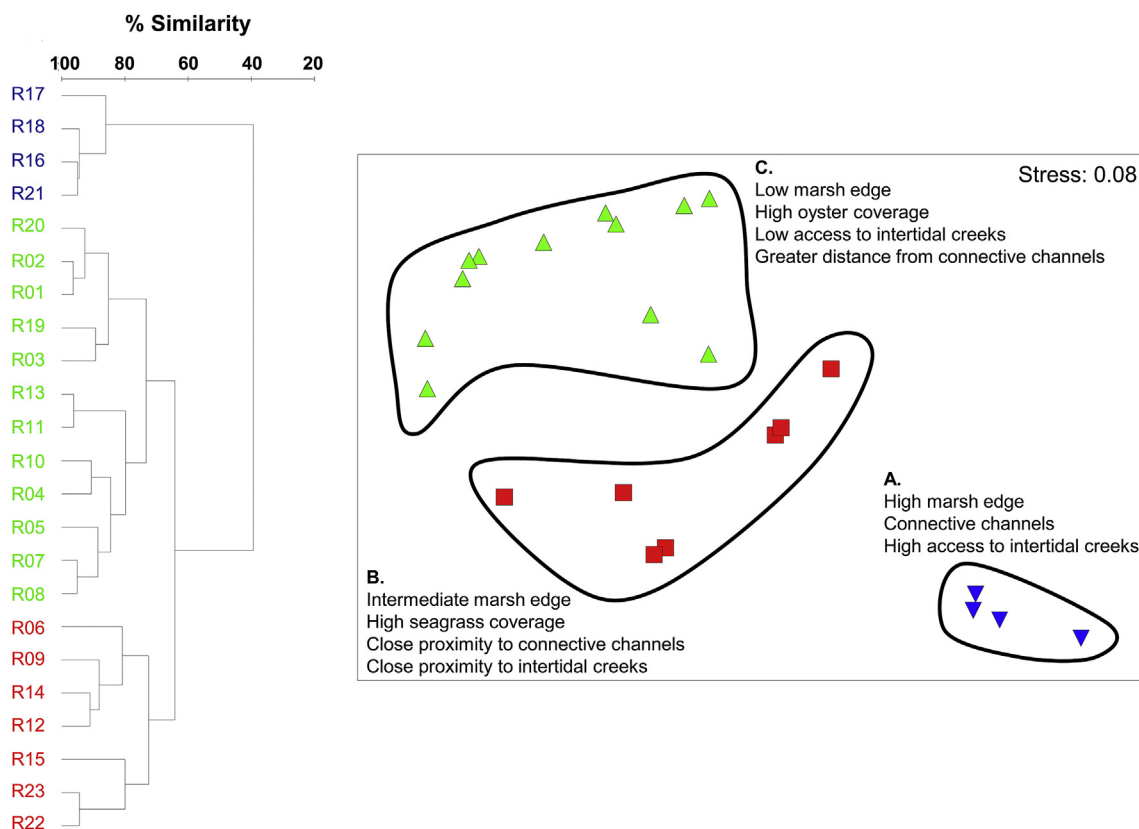
Fig. 6. Hierarchical clustering and non-metric multidimensional scaling (nMDS) showing relative similarity in habitat composition (areal seagrass coverage, aerial oyster coverage, and salt marsh edge) and connectivity (distance to connective channels, distance to intertidal creeks) among acoustic receiver listening areas (n = 23) in the bay scale array. Hierarchical cluster analysis identified three cluster groups (A. high marsh edge, B. intermediate marsh edge, and C. low marsh edge) based on 70% similarity in multivariate seascape structure.
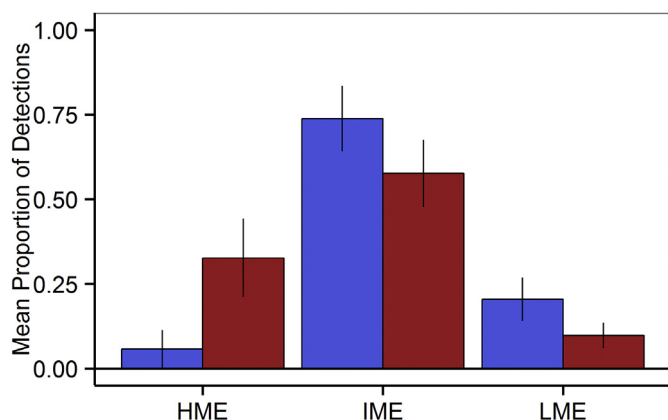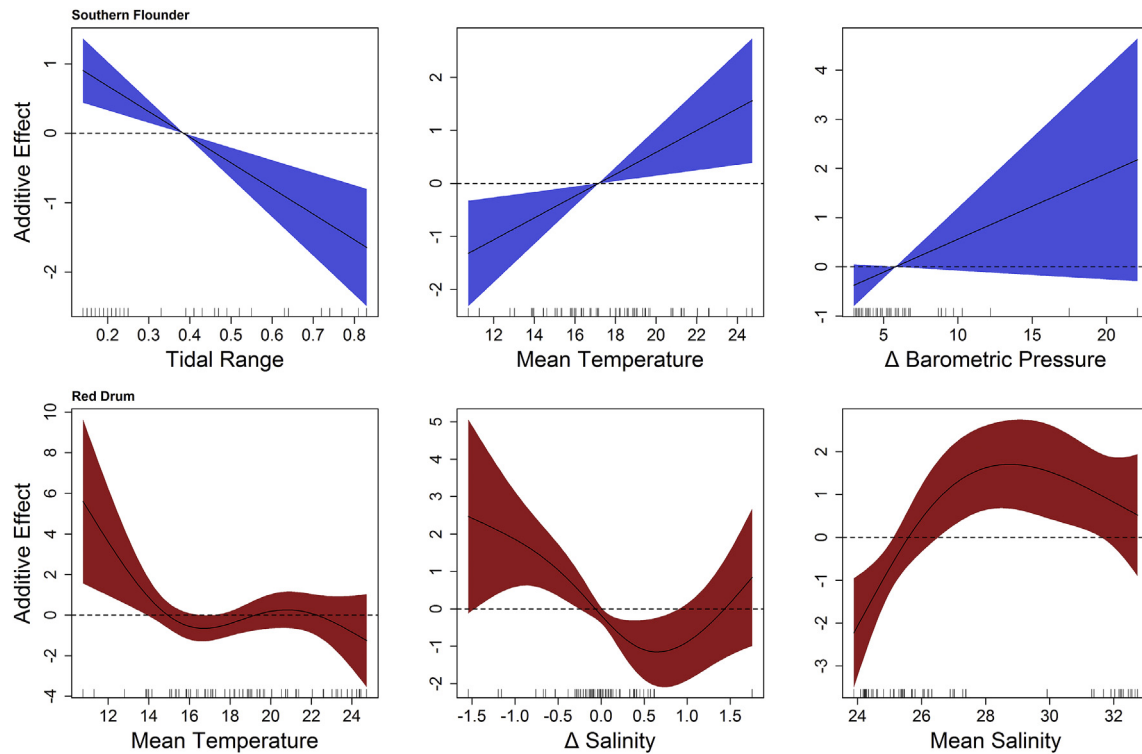

Fig. 7. Mean proportion of detections of tagged southern flounder (blue, n = 8) and red drum (red, n = 14) at receivers located in each of three habitat groupings based on 70% similarity in multivariate seascape structure among receiver listening areas at the bay scale. Receiver groupings were defined as high marsh edge (HME), intermediate marsh edge (IME), and low marsh edge (LME) seascapes, based on 70% similarity in multivariate seascape structure of receiver listening areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the removal of this variable had little impact on the final model. The final GAM for bay-scale movement of red drum included the explanatory variables temperature, salinity, and salinity variation with a percent deviance explained of 46.9% (AIC = 173.6). Salinity during the study ranged from 23 to 33 and was the most influential variable on bay-scale movement of red drum. Bay-scale movement was negatively related to salinity variation (Δ DE 14.9%, Δ AIC 9.4), with fish more active on days when salinity was decreasing; however, movements were also related to mean daily salinity (Δ DE 13.0%, Δ AIC 13.3) and were less likely to occur when salinity dropped below 25 (Fig. 8). Red drum movement was also influenced by temperature (Δ DE 10.7%, Δ AIC 5.6) but unlike southern flounder, red drum were more likely to make bay-scale movements at cooler temperatures (<16 °C).

4. Discussion

Our results indicated that juvenile southern flounder and red drum were closely associated with complex habitats (i.e. seagrasses) and their boundaries (i.e. edge) during the winter in Christmas Bay. Flounder generally prefer to bury in non-vegetated substrate (sand, mud) near structured habitat (Manderson et al., 2000; Stoner and Titgen, 2003), as these habitat boundaries often hold high densities of prey (Bologna and Heck, 2002). In the northern Gulf of Mexico, shoal grass shoot density and biomass declines precipitously in the winter (Kowalski et al., 2009) providing soft mud substrate within these senesced seagrass beds for flounder to bury adjacent to turtle grass patches and therefore potentially enhancing the value of turtle grass as suitable habitat

movement was also impacted by temperature (Δ DE 3.0%, Δ AIC 5.25), with southern flounder more likely to move at warmer temperatures (>17 °C) within the range observed (10—25 °C). Although retained by the final model, variation in barometric pressure was not a significant predictor of movement for southern flounder (p > 0.05), and Δ DE (2.4%) and Δ AIC (1.5) indicated that

Fig. 8. Response plots displaying the additive effect of environmental predictor variables on the probability of daily movement for juvenile southern flounder and red drum from final generalized additive models (GAMs) for each species. Retained variables for southern flounder GAMs include tidal range (upper left), mean temperature (upper middle), variation (Δ) in barometric pressure (upper right). Retained variables for red drum GAMs include mean temperature (lower left), variation (Δ) in salinity (lower middle), mean salinity (lower right).

for southern flounder. Conversely, the dense coverage of shoal grass present during the summer months likely limits the use of turtle grass, and previous telemetry research by Furey et al. (2013) observed that southern flounder prefer sand habitat compared to more structurally complex habitats such as seagrass during summer, supporting this hypothesis. Habitat use patterns for juvenile red drum presented here are consistent with distributional studies that link high densities of newly settled and juvenile red drum to seagrass beds (Rooker and Holt, 1997; Stunz et al., 2002; Bacheler et al., 2009). Although there are a lack of telemetry studies examining spatial use at scales comparable to the habitat scale presented here for juveniles, recent telemetry work on larger red drum (mean total length = 550 mm) in North Carolina revealed a similar affinity to seagrass and sand habitats (Fodrie et al., 2015). Thus, while direct comparisons for juvenile red drum may be limited, our results are in accord with studies on other age classes of the species, indicating that complex vegetated habitats such as seagrass beds may play an important role throughout the estuarine residency of red drum.

Variability in movement within seascapes may provide additional information on habitat use (Hitt et al., 2011; Papastamatiou et al., 2011), and here we used rates of movement measured across different habitat types and temperatures within the habitat-scale array to determine the influence of environmental conditions on dispersive behaviors of both species. Movement rates differed between southern flounder (4.0 m min^{-1}) and red drum (8.4 m min^{-1}) and the two species also exhibited varying responses to habitat type and temperature variability. Southern flounder movements were reduced with increasing habitat complexity, with rates over sand habitats higher than shoal grass and turtle grass. Interestingly, the mean rate of movement for southern flounder in or near turtle grass (1.4 m min^{-1}) was within the positioning error of the VPS (1—3 m), indicating that flounder may be nearly stationary while in close

proximity to turtle grass. This is not surprising as southern flounder are lie-in-wait predators (Burke, 1995), and their movements may be reduced when they are in or near foraging habitats that harbor higher densities of prey such as edges of turtle grass beds (Bologna and Heck, 2002). Given the observed frequent utilization of both edge and turtle grass habitat, reduced rates of movement in or near seagrass is likely reflective of juvenile flounder burying themselves in the sparse shoal grass substrate adjacent to the edge of turtle grass patches to ambush prey, a behavior that has been observed in other flatfishes (Goldberg et al., 2002). In contrast, rate of movement for red drum was not affected by habitat type, with juveniles moving at similar rates across habitats of varying complexity. Shallow estuarine habitats found in Christmas Bay are often important foraging areas for red drum (Scharf and Schlicht, 2000), and recent studies suggest that red drum are active predators that move through estuarine seascapes in search of prey (Fodrie et al., 2015). The observed similarity in movement rates of red drum across different habitats in Christmas Bay may then reflect foraging behavior of a roaming predator swimming above the submerged aquatic vegetation. Hunting modes of predator species (e.g. ambush or active) can influence the distribution and abundance of prey species; therefore, disparate foraging strategies among co-occurring estuarine predators may be important to maintaining seascape community structure and ecosystem function (Schmitz, 2008).

Variability in rates of movement between southern flounder and red drum could also be attributed to species-specific responses to changing water temperatures. Winter temperatures are highly variable in shallow sub-tropical estuaries of the northwestern Gulf of Mexico (Akin et al., 2003), and temperature within the habitat-scale array in Christmas Bay ranged from 12 to 22 °C during the study. Regression analysis showed red drum rate of movement was not affected by temperature, while southern flounder rate of

movement increased tenfold between 12 and 22 °C, suggesting that the two species respond differently to changes in temperature. Many organisms cope with thermal stress by either actively seeking more suitable habitat or passively reducing metabolic demands to conserve energy (Guderley, 2004). Previous studies have demonstrated that flatfish reduce metabolic rates, oxygen consumption, feeding activity, and movement as temperature decreases (Duthie, 1982; Lefrancois and Claireaux, 2003; Stoner et al., 2006). Therefore, reduced rates of movement by juvenile southern flounder with decreasing temperature may be a metabolic response to thermal stress. The lack of response to temperature for juvenile red drum suggests that red drum remain active at lower temperatures at the habitat scale, which may be reflective of active foraging behavior or of movement to seek more suitable habitat (i.e. deeper, warmer water) when temperature decreases, which has been suggested previously (Stunz et al., 2002; Stewart and Scharf, 2008).

Animal response to habitat features at broader geographic scales is often dependent on the composition, complexity, and spatial configuration of habitats within surrounding seascapes (Grabowski et al., 2005; Pittman et al., 2007). In the bay-scale array, juvenile southern flounder and red drum were most often detected at receivers located in heterogeneous seascapes comprised of a patchwork of complex vegetated habitats (seagrass with adjacent salt marsh and tidal creeks) and bare substrate. Bay-scale distribution of estuarine organisms is inherently influenced by spatial use at the habitat scale; therefore, it is not surprising that southern flounder and red drum often selected seascapes with seagrass due to the importance of this habitat observed in our habitat-scale array. However, broad-scale habitat selection can also be described within the context of the habitat mosaic (Grabowski et al., 2005; Dorenbosch et al., 2007), where an organism selects a particular seascape based on a spatial arrangement of habitat types that optimize foraging opportunities and/or provide shelter. Here, juvenile red drum appeared to prefer seascapes with seagrass adjacent to marsh shoreline. Tidal creeks and marsh edge are frequently utilized by red drum in other regions (Dresser and Kneib, 2007; Bacheler et al., 2009), yet were rarely utilized by juvenile red drum at the habitat scale. While seagrass may be preferred to salt marsh when both are present, previous studies have also shown that juvenile red drum are frequently found in areas where seagrass beds are adjacent to marsh edge (Stunz et al., 2002), suggesting that the spatial proximity of marsh and tidal creeks to seagrass beds may enhance habitat value (Irlandi and Crawford, 1997; Baillie et al., 2014). Our observation that receivers characterized by open bay habitat and/or oyster reef were rarely utilized highlights the relative importance of submerged aquatic vegetation to red drum (Stunz et al., 2002). However, limited detections of red drum in open bay regions may also be reflective of the influence of habitat connectivity, which is an important driver of habitat selection (Gratwicke and Speight, 2005). While both species were found more frequently in areas of at least moderate connectivity, 90% of juvenile red drum detections occurred in areas located in or in close proximity to connective channels and tidal creeks. Red drum are known to utilize subtidal creeks and channels as a temperature refuge during winter months (Adams and Tremain, 2000; Stunz et al., 2002), and connective channels located near shallow foraging areas in seagrass and marsh habitat may provide important winter habitat (Scharf and Schlicht, 2000).

Temperature may affect distributions of estuarine organisms (Akin et al., 2003), and periodic fluctuations in temperature related to meteorological events (i.e. cold fronts) were observed in Christmas Bay during the study. Although temperature was the only retained variable common to both southern flounder and red drum GAMs, response to temperature differed by species as red drum were more likely to make bay-scale movements at cooler

temperatures (<16 °C) and southern flounder were more likely to move at warmer temperatures (>17 °C). Broad-scale movements in the most basic sense are a series of directed fine-scale movements, and thus it might be expected that bay-scale movement by southern flounder would be reflective of fine-scale movement observed in the habitat-scale array, with flounder becoming more active with increasing temperature. Behavioral studies demonstrate that winter flounder *(Pseudopleuronectes americanus)* alternate between periods of resting on the seafloor and directed swimming, and the proportion of time spent swimming increases with increasing temperature (He, 2003). Similar temperature-dependent behavioral shifts have been reported for other flatfish species (Winger et al., 1999) and therefore juvenile southern flounder in Christmas Bay may exhibit a similar resting/swimming strategy. In response, the probability of southern flounder making bay-scale movement becomes more likely as temperature increases because swimming times are increased. Flatfish also feed more actively at higher temperatures and increased movement may be a result of individuals moving to better foraging habitat (Henderson et al., 2014).

Juvenile red drum are frequently found on shallow flats during summer and fall; however, it is widely accepted that these fish move to find deeper, warmer water during winter to minimize thermal stress (Adams and Tremain, 2000). Our finding of increased bay-scale movement of juvenile red drum at colder temperatures is in accord with earlier observation and is likely a response to relocate and find more suitable habitat when temperatures decrease. While juvenile red drum were less likely to make bay-scale movements at warmer temperatures, habitat-scale results suggest they remain active at smaller spatial scales. This may seem counterintuitive given the consistency in the temperature—movement relationship across spatial scales for southern flounder, but our results are in agreement with recent studies that demonstrate red drum display high site fidelity to seascapes at broad spatial scales (Dresser and Kneib, 2007), but exhibit a roving foraging behavior at fine scales within that seascape (Fodrie et al., 2015), suggesting the effect of temperature on red drum movement is dependent on spatial scale.

In addition to temperature, other physicochemical properties such as salinity and tidal cycle are known to influence movements of estuarine organisms (Childs et al., 2008; Næsje et al., 2012). The present study indicated that juvenile red drum were more likely to make bay-scale movements on days when salinity was decreasing. Declines in estuarine salinity are often the result of increased freshwater inflow following precipitation events, and decreasing salinity in Christmas Bay was typically associated with winter cold fronts during the study. These sudden changes in salinity may trigger red drum to relocate to find more suitable habitat, as similar dispersive behaviors have been described in other sciaenid fishes following cold fronts (Callihan et al., 2014). Additionally, precipitation events can cause estuarine fishes to change activity patterns and increase foraging activity (Payne et al. 2013), and red drum movement may reflect a response to shifts in prey distributions that can occur with increased freshwater inflow (Rozas et al., 2005). It is well known that tidal currents facilitate movements of estuarine organisms and influence foraging patterns of predator fish (Næsje et al., 2012), and here bay-scale movement of juvenile southern flounder was negatively related to tidal range. The finding that flounder were most likely to relocate on days with less tidal movement (tidal range < 0.4) is supported by previous telemetry research that found large scale movements of a congener, summer flounder *(Paralichthys dentatus)*, also coincided with the smallest tidal range of the month during the first quarter moon (Henderson et al., 2014). The influence of tidal range on bay-scale movement may be related to flatfish foraging behavior, as it may be

energetically beneficial for an ambush predator to remain in a location when the tidal range is large because strong tidal currents transport and supply ample amounts of prey (Capossela et al., 2013). Conversely, the lack of current when the tidal range is small may force southern flounder to move in search of prey or more suitable foraging habitat.

Assessing habitat use and movement at multiple spatial scales is critical to gaining a better understanding of fish–habitat relationships within estuarine nurseries. Our results demonstrate linkages between movement patterns and environment (biotic and abiotic) and clearly show that dispersive behaviors can vary across spatial scales and between co-occurring species inhabiting a common estuarine seascape. While southern flounder and red drum were often associated with similar habitats, differences in rates of movement within and across habitat types indicate that sympatric species may utilize habitats disparately to partition resources within a seascape. Movement and habitat use of southern flounder and red drum were influenced by physicochemical processes and seascape composition at the bay scale, yet response to these factors differed between the two species. Given the emphasis placed on ecosystem-based management, there is a growing need for studies that incorporate multi-species approaches to more effectively identify and protect habitats that are essential to ecosystem function (Hussey et al., 2015), and here we demonstrate the importance of seascape structure to sympatric fishes within an estuarine nursery.

Acknowledgments

References

Adair, S., Moore, J., Onuf, C., 1994. Distribution and status of submerged vegetation in estuaries of the upper Texas coast. Wetlands 14, 110–121.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 140–160.

Adams, D., Tremain, D., 2000. Association of large juvenile red drum, *Sciaenops ocellatus*, with an estuarine creek on the Atlantic coast of Florida. Environ. Biol. Fishes 58, 183–194.

Akin, S., Winemiller, K.O., Gelwick, F.P., 2003. Seasonal and spatial variations in fish and macrocrustacean assemblage structure in Mad Island Marsh Estuary, Texas. Estuar. Coast. Shelf Sci. 57, 269–282.

Bacheler, N.M., Paramore, L.M., Buckel, J.A., Hightower, J.E., 2009. Abiotic and biotic factors influence the habitat use of an estuarine fish. Mar. Ecol. Prog. Ser. 377, 263–277.

Baillie, C., Fear, J., Fodrie, F.J., 2014. Ecotone effects on seagrass and saltmarsh habitat use by juvenile nekton in a temperate estuary. Estuaries Coasts 1–17.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193.

Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61, 107–116.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51, 633–641.

Bologna, P.X., Heck, K., 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25, 1033–1044.

Boström, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: a review. Estuar. Coast. Shelf Sci. 68, 383–403.

Boström, C., Pittman, S.J., Simenstad, C., Kneib, R.T., 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar. Ecol. Prog. Ser. 427, 191–217.

Burke, J.S., 1995. Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. J. Fish Biol. 47, 355–366.

Callihan, J., Cowan Jr., J., Harbison, M., 2014. Sex-specific movement response of an estuarine sciaenid (*Cynoscion nebulosus*) to freshets. Estuaries Coasts 1–13.

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

Childs, A.R., Cowley, P.D., Næsje, T.F., Booth, A.J., Potts, W.M., Thorstad, E.B., Økland, F., 2008. Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. Estuar. Coast. Shelf Sci. 78, 227–236.

Clarke, K.R., Gorley, R.N., 2006. Primer V6: User Manual/tutorial. PRIMER-E, Plymouth.

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

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343.

Cowardin, L.J., Carter, V., Golet, F.C., Laroe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv. Biol. Serv, p. 131. Program FWS/OBS-79/31.

Dahlgren, C., Kellison, G., Adams, A., Gillanders, B., Kendall, M., Layman, C., Ley, J., Nagelkerken, I., Serafy, J., 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol. Prog. Ser. 312, 291–295.

Dorenbosch, M., Verberk, W., Nagelkerken, I., Van der Velde, G., 2007. Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Mar. Ecol. Prog. Ser. 334, 103–116.

Dresser, B.K., Kneib, R.T., 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. Fish. Manag. Ecol. 14, 183–190.

Duthie, G.G., 1982. The respiratory metabolism of temperature-adapted flatfish at rest and during swimming activity and the use of anaerobic metabolism at moderate swimming speeds. J. Exp. Biol. 97, 359–373.

Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F., Lowe, C.G., 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish. Res. 108, 364–371.

Fodrie, F.J., Yeager, L., Grabowski, J., Layman, C., Sherwood, G., Kenworthy, M., 2015. Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization. Oecologia 1–13.

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

Furey, N.B., Rooker, J.R., 2013. Spatial and temporal shifts in suitable habitat of juvenile southern flounder (*Paralichthys lethostigma*). J. Sea Res. 76, 161–169.

Gillanders, B., Able, K., Brown, J., Eggleston, D., Sheridan, P., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser. 247, 281–295.

Goldberg, R., Phelan, B., Pereira, J., Hagan, S., Clark, P., Bejda, A., Calabrese, A., Studholme, A., Able, K., 2002. Variability in habitat use by young-of-the-year winter flounder, *Pseudopleuronectes americanus*, in three Northeastern U.S. estuaries. Estuaries 25, 215–226.

Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86, 1926–1935.

Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol. 66, 650–667.

Grober-Dunsmore, R., Frazer, T.K., Lindberg, W.J., Beets, J., 2007. Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. Coral Reefs 26, 201–216.

Grober-Dunsmore, R., Pittman, S., Caldow, C., Kendall, M., Frazer, T., 2009. A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken, I. (Ed.), Ecological Connectivity Among Tropical Coastal Ecosystems. Springer Netherlands, pp. 493–530.

Grothues, T.M., Able, K.W., Pravatiner, J.H., 2012. Winter flounder (*Pseudopleuronectes americanus* Walbaum) burial in estuaries: acoustic telemetry triumph and tribulation. J. Exp. Mar. Biol. Ecol. 438, 125–136.

Guderley, H., 2004. Metabolic responses to low temperature in fish muscle. Biol. Rev. 79, 409–427.

He, P., 2003. Swimming behaviour of winter flounder (*Pleuronectes americanus*) on natural fishing grounds as observed by an underwater video camera. Fish. Res. 60, 507–514.

Henderson, M.J., Fabrizio, M.C., Lucy, J.A., 2014. Movement patterns of summer flounder near an artificial reef: effects of fish size and environmental cues. Fish. Res. 153, 1–8.

Heupel, M.R., Semmens, J.M., Hobday, A.J., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshw. Res. 57, 1–13.

Hitt, S., Pittman, S.J., Nemeth, R.S., 2011. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. Mar. Ecol. Prog. Ser. 427, 275–291.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E., Whoriskey, F.G., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348, 1221–1231.

Irlandi, E.A., Crawford, M.K., 1997. Habitat linkages: the effect of intertidal

saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110, 222–230.

Kowalski, J., DeYoe, H., Allison, T., 2009. Seasonal production and biomass of the seagrass, *Halodule wrightii* Aschers. (shoal grass), in a subtropical Texas lagoon. Estuaries Coasts 32, 467–482.

Lefrancois, C., Claireaux, G., 2003. Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole *Solea solea*. Mar. Ecol. Prog. Ser. 259, 273–284.

Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator–prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251, 17–39.

Mason, T.J., Lowe, C.G., 2010. Home range, habitat use, and site fidelity of barred sand bass within a Southern California marine protected area. Fish. Res. 106, 93–101.

Næsje, T.F., Cowley, P.D., Diserud, O.H., Childs, A.-R., Kerwath, S.E., Thorstad, E.B., 2012. Riding the tide: estuarine movements of a sciaenid fish, *Argyrosomus japonicus*. Mar. Ecol. Prog. Ser. 460, 221–232.

Nagelkerken, I., Sheaves, M., Baker, R., Connolly, R.M., 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish. 16, 362–371.

Nañez-James, S., Stunz, G., Holt, S., 2009. Habitat use patterns of newly settled southern flounder, *Paralichthys lethostigma*, in Aransas–Copano Bay, Texas. Estuaries Coasts 32, 350–359.

NOAA – National Oceanic and Atmospheric Association, 2012. NOAA Tide Predictions Program. Available at. co-ops.nos.noaa.gov/tide_predictions.shtml (accessed February 2014).

Papastamatiou, Y.P., Cartamil, D.P., Lowe, C.G., Meyer, C.G., Wetherbee, B.M., Holland, K.N., 2011. Scales of orientation, directed walks and movement path structure in sharks. J. Animal Ecol. 80, 864–874.

Payne, N.L., van der Meulen, D.E., Gannon, R., Semmens, J.M., Suthers, I.M., Gray, C.A., Taylor, M.D., 2013. Rain reverses diel activity rhythms in an estuarine teleost. Proc. R. Soc. B Biol. Sci. 280.

Pittman, S.J., Caldow, C., Hile, S.D., Monaco, M.E., 2007. Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. Mar. Ecol. Prog. Ser. 348, 273–284.

Powers, S.P., 2012. Age composition and distribution of red drum (*Sciaenops ocellatus*) in offshore waters of the North Central Gulf of Mexico: an evaluation of a stock under a federal harvest moratorium. Fish. Bull. 110, 283–292.

R Core Team, 2014. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. Vienna, Austria. URL. http://www.R-project.org/.

Rooker, J.R., Holt, S.A., 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: patterns of distribution and growth. Mar. Ecol. Prog. Ser. 158, 139–149.

Rooker, J.R., Simms, J.R., Wells, R.D., Holt, S.A., Holt, G.J., Graves, J.E., Furey, N.B., 2012. Distribution and habitat associations of billfish and swordfish larvae across mesoscale features in the Gulf of Mexico. PLoS One 7, e34180.

Rozas, L.P., Minello, T.J., Munuera-Fernández, I., Fry, B., Wissel, B., 2005. Macrofaunal distributions and habitat change following winter–spring releases of freshwater into the Breton Sound Estuary, Louisiana (USA). Estuar. Coast. Shelf Sci. 65, 319–336.

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

Schmitz, O.J., 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319, 952–954.

Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R., 2015. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries Coasts 38, 401–414.

Simpfendorfer, C.A., Heupel, M.R., Hueter, R.E., 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. Fish. Aquat. Sci. 59, 23–32.

Stewart, C.B., Scharf, F.S., 2008. Estuarine recruitment, growth, and first-year survival of juvenile red drum in North Carolina. Trans. Am. Fish. Soc. 137, 1089–1103.

Stoner, A.W., Titgen, R.H., 2003. Biological structures and bottom type influence habitat choices made by Alaska flatfishes. J. Exp. Mar. Biol. Ecol. 292, 43–59.

Stoner, A.W., Ottmar, M.L., Hurst, T.P., 2006. Temperature affects activity and feeding motivation in Pacific halibut: implications for bait-dependent fishing. Fish. Res. 81, 202–209.

Stunz, G.W., Linton, T.L., Colura, R.L., 2000. Age and growth of southern flounder in Texas waters, with emphasis on Matagorda Bay. Trans. Am. Fish. Soc. 129, 119–125.

Stunz, G., Minello, T., Levin, P., 2002. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25, 76–85.

Taylor, L.A., Eakins, B.W., Carignan, K.S., Warnken, R.R., Sazonova, T., Schoolcraft, D.C., 2008. Digital Elevation Model of Galveston, Texas: Procedures, Data Sources and Analysis. National Geophysical Data Center. National Oceanic and Atmospheric Administration Technical Memorandum NESDIS NGDC-12.

Vasconcelos, R.P., Reis-Santos, P., Costa, M.J., Cabral, H.N., 2011. Connectivity between estuaries and marine environment: integrating metrics to assess estuarine nursery function. Ecol. Indic. 11, 1123–1133.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381.

Winger, P.D., He, P., Walsh, S.J., 1999. Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. ICES J. Mar. Sci. J. du Conseil 56, 252–265.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.

Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. Chapman & Hall/CRC, Boca Raton, FL.

Wood, S.N., 2008. Fast stable direct fitting and smoothness selection for generalized additive models. J. R. Stat. Soc. Ser. B 70, 495–518.