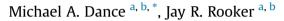
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Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery



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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 habitatscale (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 ($>17 \circ C$), 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 multispecies assessments for improving our understanding of habitat value and ecosystem function.

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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





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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 fishhabitat (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 bayscale (>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 (\sim 26 km²) 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, nonvegetated 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 bayscale 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

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