

SPATIO-TEMPORAL VARIABILITY IN MOVEMENT PATTERNS AND HABITAT
ASSOCIATIONS OF JUVENILE FISHES IN ESTUARINE SEASCAPES

A Dissertation

by

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ABSTRACT

Understanding the ecological value of nursery habitats is important to the conservation of coastal fisheries. The purpose of this research was to address gaps in our knowledge of nursery habitat value for both juvenile red drum (*Sciaenops ocellatus*) and southern flounder (*Paralichthys lethostigma*) within estuarine seascapes in Texas. Acoustic telemetry and habitat suitability models were used to identify spatial and temporal variability in habitat associations and movement patterns of both species. Objectives were to determine the influence of biotic factors on transmitter performance in acoustic telemetry studies, examine habitat use and movement patterns of both species at two spatial scales (habitat and bay scale) within a model estuary, and to use generalized additive models (GAMs) to evaluate ontogenetic and regional variation in habitat suitability for red drum along the Texas coast.

Significant differences in detection probability (2-7 fold differences) were observed between internally and externally placed transmitters on red drum as well as between transmitters attached externally to red drum and those attached to a fixed line, while no species effect was observed for internal transmitters in red drum and southern flounder. At the habitat scale (1 m – 1 km), both species were associated with seagrass and edge habitat; however, rates of movement differed greatly between species, which likely reflected the use of different foraging strategies (i.e. ambush vs. active). Bay-scale (1-20 km) distribution was influenced by physicochemical conditions and seascape composition, with both species found most frequently in areas with high seagrass

coverage and in close proximity to tidal creeks and connective channels. At broader, regional scales, stage-specific habitat suitability models demonstrated that fish-habitat relationships for juvenile red drum were often similar among estuaries along a latitudinal gradient; however, the relative importance of abiotic and biotic factors to red drum distribution and abundance varied, suggesting that habitat quality within each life stage may be determined by variables that have the greatest impact on survival within a particular estuary. Results of this research demonstrate that habitat use and movement patterns of estuarine fish are scale dependent and vary both spatially and temporally within and among estuarine nursery areas.

DEDICATION

I dedicate this work to my parents and grandparents who have sacrificed so much for me, and have been unwavering in their support and interest in my studies since I was a boy.

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CHAPTER I

INTRODUCTION

Estuaries are highly productive ecosystems found worldwide at the interface of terrestrial and marine environments (Barbier et al., 2011). These dynamic environments are used by a wide range of organisms but are vulnerable to anthropogenic impacts due to their proximity to growing coastal development (Able, 2005; Barbier et al., 2011). This is of particular concern because estuaries serve as nurseries for many fishes and invertebrates, and conservation of estuarine ecosystems may be vital to maintaining valuable marine fisheries (Beck et al., 2001; Worm et al., 2006). Within estuarine landscapes (referred to hereafter as “seascapes”) are several benthic habitat types (e.g. seagrasses, oyster reefs, salt marsh, mangroves) that provide structure for juvenile fishes and invertebrates (Boström et al., 2011). Therefore, conservation efforts have focused on identifying critical nurseries, defined as those habitats or areas within estuaries that contribute a disproportionately larger portion of recruits to adult populations (Beck et al., 2001; Dahlgren et al., 2006). As a result, the value or quality of presumed nursery habitats is often assessed by contrasting estimates of density, growth, and survival of individuals from different habitats (Able, 2005).

Nursery habitats presumably maximize growth and survival by providing food as well as refuge from predators (Rooker et al., 1998; Minello et al., 2003). Mobile taxa often use a network of habitats that are functionally linked by direct animal movement and/or transfer of organic material across habitat boundaries. These linkages are poorly

understood for many estuarine fishes because they are subject to variable environmental conditions that can lead to shifts in habitat use (Sheaves et al., 2015). Thus, habitat use and movement patterns of juvenile fishes in estuaries can vary seasonally, or even across daily cycles (diel or tidal), making identification of nursery habitat difficult (Gillanders et al., 2003, Sheaves et al., 2015).

Many species spend only a portion of their early life in estuaries, and the duration of estuarine residency is variable and can range from months to years (Able, 2005). For species residing in the estuary for multiple years, dietary needs and predation vulnerability shift ontogenetically with increasing size and mobility, and thus several habitats or seascapes are often needed to complete the life cycle (Gillanders et al., 2003). Determining the relative value of nursery habitat for such species is often compromised because of the lack of data connecting habitat requirements across multiple life stages (Sheaves et al., 2015). Considerable effort has been devoted to studies assessing growth and survival of juvenile fish at settlement into estuarine habitats; however, our understanding of the degree to which habitat requirements change with ontogeny is extremely limited despite the fact that survival at this stage may be habitat dependent (Gillanders et al., 2003).

The purpose of this dissertation was to use complementary approaches to examine spatial and temporal shifts in habitat requirements and movement patterns for juvenile fishes in estuarine nurseries in Texas. Given that this research relied heavily on acoustic telemetry, I first tested fundamental assumptions of this methodology for examining habitat use and movement patterns of juvenile fishes. Specifically, I

examined the impacts of transmitter placement and species on detection efficiency of two different finfish: red drum (*Sciaenops ocellatus*) and southern flounder (*Paralichthys lethostigma*). I then use acoustic telemetry to characterize habitat use and connectivity at two spatial scales (habitat, bay) for red drum and southern flounder within a model estuary. Finally, a generalized additive model framework was used to contrast ontogenetic shifts in fish-habitat relationships for juvenile red drum across three estuaries along a latitudinal gradient on the Texas coast.

The overall objective for this study was to evaluate spatio-temporal variability in habitat associations, distribution, and abundance within estuarine nurseries and to determine the influence of environment, spatial scale, and species on movement patterns of juvenile fish within and among estuarine seascapes. The specific objectives of each chapter are listed below:

Chapter II.

1. Examine the effects of transmitter placement (internal vs. external) on detection range of a common estuarine finfish, red drum
2. Assess the impact of the host animal (red drum) on detection range by comparing detection range of a transmitter fixed to a line to that of a transmitter attached to an animal
3. Compare detection range of internal transmitters on red drum to another common estuarine fish that differs in body type, southern flounder, which has a laterally compressed body relative to red drum

Chapter III.

1. Characterize both habitat-scale (< 1 km) and bay-scale (> 1 km) patterns of habitat use for juvenile southern flounder and red drum
2. Identify environmental processes influencing movement and habitat selection of each species

Chapter IV.

1. Examine the influence of biotic and abiotic factors on the distribution and abundance of juvenile red drum for three estuarine systems (Galveston, Aransas-Corpus Christi, and Laguna Madre) that differ in benthic habitat composition, hydrology, and physicochemical conditions
2. Identify shifts in these relationships between two stages in the first year of life that are potential bottlenecks in recruitment success of marine fishes, settlement and the first winter

CHAPTER II

DOES TRANSMITTER PLACEMENT OR SPECIES AFFECT DETECTION EFFICIENCY OF TAGGED ANIMALS IN BIOTELEMETRY RESEARCH?

Introduction

The study of animal movement is rapidly increasing amid growing efforts to assess the effects of habitat loss/fragmentation and climate change on animal distributions (Nathan et al., 2008; Schick et al., 2008). Animal movement patterns can provide researchers with a better understanding of how animals interact with their environment across a range of spatial and temporal scales (Morales and Ellner, 2002; Patterson et al., 2008; Morales et al., 2010). In recent years, technological advances in biotelemetry and geographic information systems have greatly improved our ability to track animals and relate patterns of movement to their environment (Cooke et al., 2004; Cagnacci et al., 2010; Hussey et al., 2015). Although the study of animal movement has progressed rapidly in a relatively short period of time, studies identifying potential uncertainty and limitations associated with animal tracking technologies are lacking and are needed to improve interpretations of movement data (Frair et al., 2010; Fieberg et al., 2010).

The ability of researchers to characterize animal movements is considerably impaired in aquatic systems, and acoustic telemetry has quickly become a powerful tool to examine movement patterns of marine and freshwater taxa (i.e. fishes, crustaceans, cephalopods, mammals) (Donaldson et al., 2014; Hussey et al., 2015). Acoustic

receivers can be deployed in a variety of configurations to address different research questions and range in size from small arrays to examine site fidelity to a particular habitat, to mesoscale gridded arrays for estimating home range and activity spaces across larger water bodies (i.e. bays, lakes), to widely dispersed receiver lines (i.e. curtains or gates) deployed at intervals along a coast or river to monitor fish passage associated with broad movements or migrations (see Heupel et al., 2006). In addition, recent advancements have given researchers the ability to deploy high-density arrays of receivers with overlapping listening areas (acoustic positioning systems) to triangulate animal positions and provide fine-scale animal tracks (Espinoza et al., 2011; Grothues et al., 2012; Furey et al., 2013). Despite the increase in acoustic telemetry studies over the last decade (Kessel et al., 2014), our understanding of the range at which receivers can detect transmitters is still surprisingly limited. This discrepancy between application and understanding can lead to poorly designed receiver configurations and ultimately misinterpretation of acoustic telemetry data (Payne et al., 2012; Gjelland and Hedger, 2013).

A variety of factors can affect the ability of acoustic receivers to detect transmitters including environmental and meteorological conditions (Gjelland and Hedger, 2013), ambient noise (Welsh et al., 2012), biofouling (Heupel et al., 2008), transmitter type/power (How and de Lestang, 2012; Cagua et al., 2013), depth (Gjelland & Hedger, 2013), and diel (Payne et al., 2010) or tidal (Mathies et al., 2014) cycles. The influence of many of these factors varies across systems, and thus it is generally recommended that researchers conduct range tests within a study site prior to, and/or

during, a study to estimate the distance from a receiver in which a tag can be reliably detected within an array (Heupel et al., 2006; Payne et al., 2010). The majority of range tests are aimed at determining the impact of environmental variables, and therefore detection range is typically estimated from fixed transmitters in water despite the fact that the most common method of attachment for fish is to surgically implant the transmitter into the coelomic cavity rather than attaching it externally (Cooke et al., 2011). Thus, range tests are largely conducted under the assumption that transmitter performance in water will not differ from the tag performance when internally implanted within or externally attached to the host animal (Kessel et al., 2014). Moreover, if the body wall of the tagged animal does indeed affect transmission, it might then be further expected that these effects would be dependent upon morphology. Nevertheless, our understanding of the effect the tagged organism (or tagging method) has on detection range of acoustic transmitters is currently lacking.

Here I use an experimental approach to test the effect of three biotic factors affecting acoustic telemetry studies. We first examined the effects of transmitter placement (internal vs. external) on detection range of a common estuarine finfish, red drum (*Sciaenops ocellatus*). Next, we assessed the impact of the host animal (red drum) on detection range by comparing detection range of a transmitter fixed to a line to that of a transmitter attached to an animal. Lastly, we compared detection range of internal transmitters on red drum to another common estuarine fish that differs in body type, southern flounder (*Paralichthys lethostigma*), which has a laterally compressed body (“flatfish”) relative to red drum.

Methods

Experiments were conducted in the spring and fall of 2013 in Galveston Bay, a large estuary in the northern Gulf of Mexico. Benthic structure of the study site was homogenous, and characterized by bare sand substrate and relatively uniform depth [1.02 ± 0.03 m (mean \pm SE)]. Tagged fish and transmitters used in experiments were placed inside a 1-m³ enclosure comprised of a polyvinyl chloride (PVC) frame and plastic mesh that was secured to a PVC pole at the origin of a line of receivers (Vemco VR2W) attached to fixed moorings located 0, 50, 100, 150, 200, 250, 300, 400, 500, and 600 m from the enclosure (Figure 1). This structure allowed for movement of tagged individuals within a restricted area to account for some natural variability in detection probability due to fish movement and orientation, while also controlling for transmitter location and preventing predation. Receivers (n=10) were attached (hydrophone facing up) to the lower end of 2 m sections of PVC. The location of all receivers was randomized for each replicate trial to reduce the effects of individual receiver performance on detection range (Heupel et al., 2008).

Red drum was chosen as a model fish species and was used in all three experiments, while southern flounder was used as a contrasting species in the third experiment. Both species have been previously used in telemetry studies (Furey et al., 2013; Fodrie et al., 2015) and co-occur over much of their range. Individuals were captured via hook and line and held in 1.7 m³ tanks in the Texas A&M University Sea Life Center. Fish were anaesthetized with clove oil prior to tagging and fitted with Vemco V9-1H coded transmitters (69kHz, 9 mm diameter x 24 mm length, 151 dB) with

a nominal delay of 15 sec (range 10-20 sec). V9 transmitters are commonly used to study movement patterns of fishes and invertebrates in a range of systems (e.g. Welch et al., 2011; Bloor et al., 2013; McMahan et al., 2013). External tagging followed a protocol modified from Furey et al. (2013) in which each transmitter was fixed to a vinyl Peterson disc tag (FloyTag Inc) with heat shrink wrap and mounted to the dorsal musculature of the fish. Two sterilized nickel pins held in place by another vinyl Peterson disc tag were passed through the dorsal musculature and secured to the vinyl disc tag holding the transmitter with rubber earring backings and a metal crimping sleeve. Internal transmitters were surgically implanted into the coelomic cavity via a small ventral incision and closed with one or two interrupted sutures (4-0 Ethicon vicryl). Overall, six V9-1H transmitters were used in the study and transmitter pairings for each trial were rotated to minimize the effect of any individual transmitter on detection range.

To test the effects of internal versus external placement on transmitter performance, we conducted replicate trials on five consecutive days with similar environmental conditions. Prior to each trial, a single red drum (55.9 ± 1.5 cm; mean \pm SE) was fitted with both an internal and external V9-1H transmitter and placed in the field enclosure after a recovery period (minimum 1 hour). Receivers (random order) were then deployed at the fixed moorings located at set distances from the enclosure (0, 50, 100, 150, 200, 250, 300, 400, 500, and 600 m; see Figure 1). Data were recorded for approximately three hours, after which the fish and receivers were recovered and data were uploaded. Five V9-1H transmitters were used for this experiment and the pairing of

transmitters used in each trial was unique. No transmitter was used more than twice as either an internal or external transmitter.

The second experiment tested for differences in detection range between transmitters on an animal host (red drum) and attached to a fixed line. This experiment followed a similar procedure to the first, with the exception that red drum (TL: 55.0 ± 3.0 cm) were fitted with only an external transmitter and placed in the enclosure with a fixed transmitter that was suspended from the top of the enclosure via monofilament line 0.5 meters above the substrate (Figure 1). A unique red drum was used for each of the three replicate trials, with receiver location and transmitters again randomized for each trial. Because we were unable to conduct this experiment on consecutive days, each trial lasted 24 hours to account for the variability in weather conditions and daily cycles (tide, day/night) among replicates ($n = 3$).

The third experiment tested for differences in detection range between red drum and southern flounder, two species that differ in body morphology and behavior. Prior to each trial, a single red drum (39.8 ± 4.5 cm; total length \pm SE) and southern flounder (39.8 ± 2.9 cm) of similar size were fitted with internal transmitters and placed in the enclosure (Figure 1). The rest of the trial followed a similar procedure described previously for the other two experiments, with the exception that detection range was tested to 400 m (set distances of: 0, 50, 100, 150, 200, 250, 300, 400 m) rather than 600 m. Unique red drum and southern flounder were used for each of five replicate trials, with receiver order and transmitters randomized before each trial. Similar to the second experiment, we were unable to conduct the experiment on consecutive days, and

therefore, we used 24-hour time periods to account for variability in weather conditions and daily cycles between days.

The number of transmitter detections recorded per receiver during each trial was converted to a detection probability by dividing the number of detections at a given receiver by the number of detections recorded by the receiver at the origin (0 m). Analysis of covariance (ANCOVA) was used to test the variation in the relationship between detection probability and distance among treatment groups for each of the three experiments. Detection probability was the dependent variable for each ANCOVA model with transmitter treatment as the independent variable and distance from transmitter as the covariate. In each case, preliminary models were run first (slopes test, interaction-regression) to determine if slopes of the regression lines differed between treatments. The main effects test of the ANCOVA (y-intercept) was only performed for experiments in which the assumption of parallel slopes was met. Mean differences in detection probability between paired samples in each experiment was assessed with paired t-tests to determine the magnitude and specific distances at which differences occurred in each experiment. Adjusted p values (q value) were used to control the false discovery rate (FDR) at $\alpha = 0.05$ (Benjamini and Hochberg, 1995), which is the preferred adjustment to correct for multiple comparisons in ecological studies (Nakagawa, 2004; Pike, 2011). Although it is generally acceptable to use the uncorrected p-value in this case, given that each comparison tested a different distance-specific null hypothesis (Cabin and Mitchell, 2000), we present both corrected and uncorrected values. We then calculated effect size for each paired comparison using Cohen's d

(Cohen, 1992) to examine the magnitude of the treatments tested, where effect size magnitudes are: negligible ($d < 0.2$), small ($d = 0.2 - 0.5$), medium ($d = 0.5 - 0.8$), and large ($d > 0.8$).

Results

Detection probability declined with increasing distance from transmitter for all experiments. Mean detection probability was significantly greater for external transmitters than internal transmitters (ANCOVA y-intercept; $P < 0.001$), and ranged from 1.00 (50 m) to 0.38 (600 m) for external transmitters compared to 0.93 (50 m) to 0.07 (600 m) for internal transmitters. External transmitters outperformed internal transmitters in paired comparisons at all distances in every trial (see Table 1, Figure 2), and mean differences in detection probability between paired external/internal transmitters at each distance ranged from a minimum of 0.06 at 50 m to a maximum of 0.64 at 300 m. Differences in detection probability were significant between treatment pairs at all distances greater than 100 m (paired t-tests; $P < 0.05$), with external transmitters detected 2-7 times more frequently at these distances (Figure 2). While large effect sizes were observed for all comparisons (Cohen's $d > 1.3$), smaller but consistent differences in detection probability between internal/external pairs at 50 m (mean difference = 0.06) and 100 m (0.35) were not deemed to be significant (paired t-tests; $P > 0.05$).

The rate of decline in detection probability as a function of distance differed between transmitters attached to an animal host (red drum) and those attached to fixed

line (ANCOVA slopes test; $P < 0.01$), with transmitters on red drum detected less frequently as distance increased. Mean detection probability ranged from 1.00 (50 m) to 0.47 (600 m) for transmitters attached to the line, and from 1.00 (50 m) to 0.25 (600 m) for transmitters externally attached to red drum. While transmitters performed similarly between 50 and 150 m (mean paired difference < 0.05 m), transmitters attached to the line were consistently detected more frequently than transmitters on red drum at distances greater than 150 m (range: 0.14-0.26, Table 1, Figure 3). We also observed very large effect sizes at most distances ($d > 1.5$), yet despite the magnitude of these differences, paired comparisons at each distance indicated that transmitter treatments were significantly different at only two distances: 300m and 500m (paired t-tests; $P < 0.05$), and no differences were detected at any distance after controlling for FDR ($q > 0.05$) (Table 1).

Red drum and southern flounder were used as model species to test for species-specific differences in detection range. The width of the body wall was thicker in red drum (3.3 ± 0.7 mm; mean \pm SE) than in southern flounder (0.5 ± 0.1 mm). Still, detection probability for transmitters internally placed in red drum and southern flounder did not differ statistically (ANCOVA y-intercept test; $P > 0.05$). Mean detection probability ranged from 0.99 (50 m) to 0.08 (400 m) for red drum and from 0.99 (50 m) to 0.05 (400 m) for southern flounder. Examination of differences in paired treatments indicated that transmitters placed in southern flounder were often detected more frequently at closer receivers (< 150 m) than transmitters placed in red drum (Table 1, Figure 4). However, differences in detection probability between the two species were

variable across the 5 trials, and no significant differences in detection probability were found at any distance (paired t-tests; $P > 0.05$).

Discussion

Here we demonstrate that the placement of acoustic transmitters affects their performance, with detection probabilities of external transmitters on red drum being 2 to 7 fold higher than internal transmitters at receiver distances $> 100\text{m}$. This finding suggests that intracoelomic implantation of acoustic transmitters in fish may reduce the detection range of transmitters. Our results are in accord with previous studies that reported reductions in detection efficiency and/or signal strength associated with internal transmitters in both radio-telemetered finfish (Cooke and Bunt, 2001) and acoustically-tagged cuttlefish (Jackson et al., 2005). In fact, cuttlefish simultaneously tagged with internal and external transmitters were detected four times more efficiently with the external transmitter (Jackson et al., 2005), which is similar to our findings and suggests that signal attenuation likely occurs at a higher rate for acoustic transmitters placed inside the body cavity of the host species.

While the exact mechanism of signal attenuation is unknown, submerged aquatic vegetation, biofouling, mineralized hard parts, and several different biological tissues have all been shown to reduce the detectability of acoustic transmissions (Jackson et al., 2005; Heupel et al., 2008; Wilson et al., 2013). Still, any reduction in detection range caused by intracoelomic implantation of acoustic transmitters is widely assumed to be negligible, because the density and sound properties of animal tissues are thought to be

similar to that of water (Kessel et al., 2014). This may be true for tissues with high water content, as acoustic attenuation is negatively correlated to tissue water content and those tissues with high water content are more likely to have similar sound properties to water (Olerud et al., 1990). However, attenuation is positively correlated with collagen concentration in tissue (O'Brien, 1977; Olerud et al., 1990; Mast, 2000), and therefore we might expect tissues with higher collagen content such as bones, tendons, and fish scales to have higher acoustic impedance (Pohlhammer and O'Brien, 1980), potentially increasing signal attenuation from transmitters placed in the body cavity of the host animal. While we cannot unequivocally determine the direct cause of the observed reduced detection range for internal transmitters in this study, the consistent and substantial difference in detection probability between internal and external transmitters across a range of distances suggests that traditional range tests of transmitters, which are often performed by attaching the transmitter to a fixed structure, will overestimate the detection range of surgically implanted transmitters.

The detectability of acoustic transmitters can also be influenced by the behavior of the study animal (Heupel et al., 2006; Grothues et al., 2012), and therefore the movement or orientation of a tagged animal may likewise impact detection range. Our second experiment showed that detection probability declined more rapidly for transmitters attached to an animal host relative to transmitters attached to a fixed line. This finding suggests that attaching transmitters to fixed or stationary objects during range tests may not accurately represent the detection range of externally tagged animals *in situ*. Coupling this result with findings from our first experiment showing reduced

performance for internally placed transmitters, it is likely that conventional range testing (i.e., transmitter attached to a nonliving object) considerably overestimates the detection range achieved for internally tagged fish or other animal hosts. In the current study, tagged red drum were free to move within a limited area inside the experimental enclosure, and observed differences in detection probability between transmitters attached to red drum and the fixed line were likely reflective of red drum movement or orientation within the enclosure. Similarly, other studies have shown that animal orientation or transmitter movement can negatively affect the accuracy of acoustic telemetry systems (Espinosa et al., 2011; Grothues et al., 2012).

Given the observed reduction in detection range for internal acoustic transmitters in the first experiment, it might be expected that variation in body type between red drum and southern flounder would lead to differences in transmitter performance. Multi-species acoustic telemetry studies are increasingly utilized to examine species interactions (Speed et al., 2011; McMahan et al., 2013; Hussey et al., 2015), and the ability to make comparisons between or among species is dependent on the assumption that internal transmitters perform similarly among species. In the current study, we observed that detection range was statistically similar between these two species even though their body types differ markedly, suggesting that species-specific differences in detection range may be minimal. Moreover, the similarity in detection range between two species with a threefold difference in body wall thickness makes it seem unlikely that the thickness of the body wall is the sole mechanism reducing detection range of internal transmitters relative to externally attached transmitters. Although we did not

detect species-specific differences in the current study, it is possible that we were unable to detect differences that may actually occur *in situ* due to behavioral differences in the two species. The enclosure likely precluded fish from natural behaviors (i.e. active swimming, burying, association with submerged aquatic vegetation, etc.) that could affect transmitter performance (see Grothues et al., 2012), therefore reducing our ability to detect behavior related differences. Future studies that examine the influence of swimming speed, position in the water column, or habitat preference on detection range would be beneficial to our understanding of the impacts of species-specific behavior on transmitter performance.

A variety of factors can affect the detection range of acoustic transmitters (Kessel et al., 2014), and it is possible that relationships described here could vary across different transmitter types or ecosystems. Previous studies have shown that transmitter type and power output impacts detection range (How and de Lestang, 2012), and thus it is possible that transmitters with a higher or lower power output than those used in this study may not respond in the same manner. Nonetheless, the conspicuous difference in detection range for internal and external transmitters presented here suggest a similar effect is likely for other transmitter types (i.e. power outputs), although further testing would be needed to determine the magnitude of this effect. Detection range for our transmitters attached to a fixed line (> 50% detection probability at 500 m) was comparable to or exceeded reported detection ranges (150-500 m) for fixed transmitters of similar power output in previous estuarine or coastal studies (Chittendon et al., 2008; Sulak et al., 2009; Francis, 2013) and far exceeded that of transmitters in reef systems

(50-150 m) (How and de Lestang, 2012; Welch et al., 2012). Because detection range can vary across systems of varying complexity and depth (i.e. reefs, coastal, riverine, offshore), there may be variability in the magnitude of the effects of the host animal on detection range. However, comparisons to previous studies also suggest that our system may represent a favorable acoustic environment and the reduction in detection range associated with transmitter placement shown here could be conservative relative to systems with greater influence from environmental factors that attenuate acoustic signals (e.g. noise, wind/sea surface variability, depth).

Our results highlight the value of *in situ* range testing using animal hosts and suggest that the use of external transmitters may be beneficial, depending on the research aims of the study, as it will likely improve detection range. Still, the use of internal transmitters is often advantageous to other research goals (i.e. increased study duration) and intracoelomic implantation remains the most common attachment method in fish. Therefore, in such instances, researchers should consider range testing with an internally tagged animal to provide the most realistic estimates of detection range for transmitters *in situ*. Because it is not always feasible to use animals during range testing, caution should be used when interpreting traditional range tests, particularly during the planning phase of studies that deploy arrays such as curtains, gates, and acoustic positioning systems that rely on receiver spacing to effectively cover an area of interest (see Heupel et al., 2006, Espinoza et al., 2011). Overestimation of detection range can lead to inadequate receiver spacing and reduced detection efficiency, ultimately impairing the ability of researchers to detect movement patterns, fish passage, and fish-habitat

relationships. Given the increasing utilization of acoustic telemetry as a tool to monitor animal movements in aquatic environments, it is important that we are able to accurately interpret animal locations, and here we demonstrate that considering the impacts of transmitter placement on detection range will help improve study design and data interpretation of future acoustic telemetry studies.

CHAPTER III

HABITAT- AND BAY-SCALE CONNECTIVITY OF SYMPATRIC FISHES IN AN ESTUARINE NURSERY*

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, 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 the juvenile life stage, 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 within a

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seascape for estuarine taxa 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 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 lacks 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; Nañez-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 et al., 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 processes 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.

Methods

The study was conducted in Christmas Bay, which is a small (~26 km²) sub-bay located at the southwestern extreme of the greater Galveston Bay Estuary (GBE) in the northwestern Gulf of Mexico (Figure 5). Christmas Bay is utilized by both species (Furey et al., 2013; Stunz et al., 2002a) 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 substantial 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 (primarily 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 (Figure 5B). 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 1m - 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 (Figure 5C). 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 (Figure 5C). Synchronizing transmitters or “sync tags” (Vemco V9-1H, 69kHz) 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 (Figure 5B). 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 (Figure 5).

Benthic habitats (salt marsh edge, tidal creek, oyster, seagrass, channel, sand) 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). Sub-tidal channels connecting Christmas Bay to surrounding bays 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 was 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 minutes in the habitat-scale array ($n = 6$) and every 30 minutes 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 minute 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, 69kHz) with a nominal code transmission delay of 120 s (range: 60-180s). Prior to tagging, individuals were kept in 0.7 m³ tanks at the Texas A&M University at Galveston 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 hours 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.

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 \pm 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 minutes were also omitted from habitat-scale analysis to minimize the influence of release location on fish positions. Likewise, detections within the first 6 hours were removed from the bay-scale analysis 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 (shoal grass, turtle grass, oyster, sand, or salt marsh) 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 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 displayed non-random use.

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 minutes. 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 12-22° 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 aerial 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) 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 (Δ DE) and AIC (Δ AIC) 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).

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 (3661, 3663) after data filtering; therefore, these individuals were not used in EDA analysis at the habitat scale (Table 2).

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; $p > 0.05$) (Figure 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; $p > 0.05$) (Figure 6). 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 ($8.4 \pm 0.5 \text{ m min}^{-1}$; mean \pm SE) than southern flounder ($4.0 \pm 0.1 \text{ m min}^{-1}$) 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 ($1.4 \pm 0.1 \text{ m min}^{-1}$) relative to both sand ($6.9 \pm 0.2 \text{ m min}^{-1}$) and shoal grass habitats ($3.0 \pm 0.1 \text{ m min}^{-1}$) (Tukey's HSD; $p < 0.01$; all comparisons) (Figure 7). 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 $1 \text{ }^{\circ}\text{C}$ (regression; $p < 0.01$) (Figure 8). 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 acoustic receiver listening areas (Figure 9). 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 (Figure 10). 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 unvegetated 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; $p > 0.05$) (Figure 11). 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 \pm SE) for southern flounder and from 2.0 to 63.5 km (12.4 ± 4.7 km) for red drum. Maximum daily movement in one day was 3.2 km for southern flounder (1.2 ± 0.4 km; mean \pm 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 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 movement on days with little tidal variation (< 0.4 m) (Figure 12). Bay-scale movement was also impacted by temperature (Δ DE 3.0%, Δ AIC 5.25), with southern flounder more likely to move at warmer temperatures ($> 17^\circ\text{C}$) within the range observed (10 to 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 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 23-33 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 (Figure 12). 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 ($< 16^{\circ}$ C).

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 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., 2002a; 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 12-22°C during the study. Regression analysis showed red drum rates of movement were 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 Clarieaux, 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., 2002a; 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; Bachelier 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., 2002a), 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. 2002a). 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., 2002a), and connective channels located near shallow foraging areas in seagrass and marsh habitat may provide important winter habitat (Scharf and Schlight, 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 ($< 16^{\circ}\text{C}$) and southern flounder were more likely to move at warmer temperatures ($> 17^{\circ}\text{C}$). 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 an 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.

CHAPTER IV
STAGE-SPECIFIC VARIABILITY IN HABITAT ASSOCIATIONS OF JUVENILE
RED DRUM ACROSS A LATITUDINAL GRADIENT

Introduction

Estuaries provide important habitat for a wide variety of marine organisms during early life, and are generally thought to serve as nursery areas for coastal ecosystems (Beck et al., 2001; Gillanders et al., 2003). Because subtle fluctuations in growth and survival during early life can greatly affect recruitment to adult populations, there is considerable interest in identifying estuarine habitats that improve growth and survival of juvenile fishes and invertebrates (Able, 2005; Dahlgren et al., 2006). Currently, many estuarine habitats are in decline due to degradation or alteration and thus, there is need to identify “high quality” habitat for many coastal taxa (Boström et al., 2011). While benthic habitats such as seagrass, mangroves, oyster reef, and salt marsh are known to hold disproportionately higher densities of juvenile fishes and invertebrates (Boström et al., 2006), assessing the relative value of these habitats across broad spatial scales is often difficult, as habitat quality is influenced by a variety of abiotic and biotic factors that vary spatially and temporally in estuarine systems (Sheaves et al., 2015).

Habitat suitability models are increasingly used to identify factors influencing the distribution of juvenile organisms and have recently been used to classify potentially important nursery areas in estuarine ecosystems (Guisan and Thuiller, 2005; Niklitschek

and Secor, 2005). While species-habitat relationships are often broadly applied across a large geographical area (Johnson et al., 2013), the complex and variable nature of these relationships realistically limits our ability to extrapolate them across both time and space (McAlpine et al., 2008). For many marine fishes, habitat requirements change with ontogeny (Bartolino et al., 2011; Johnson et al., 2013). Likewise, the degree to which these relationships vary geographically is poorly understood, despite the fact that neighboring estuarine systems may differ in climate, hydrology, physicochemical processes, and anthropogenic impacts. Therefore, spatially explicit approaches that account for multiple life stages may be needed to more effectively assess habitat quality and identify highly suitable habitats within a particular estuarine system.

Here, a generalized additive model (GAM) framework was used to examine stage-specific habitat relationships for juvenile red drum (*Sciaenops ocellatus*) in three estuaries along a latitudinal gradient in the northwestern Gulf of Mexico. Red drum are estuarine dependent sciaenids of considerable economic value, and are among the most highly targeted recreational finfish in the GOM (Coleman et al. 2004). Adult red drum typically spawn in coastal waters near tidal passes in the fall, with juveniles settling in estuarine habitats, where they remain throughout adolescence (ca. 0-3 years) before joining adult populations in coastal waters (Powers et al., 2012). Differences in density, survival, and growth have been observed among estuarine habitats for newly settled red drum (Rooker and Holt, 1997; Rooker et al., 1998; Stunz et al., 2002b), suggesting that nursery value may vary greatly among habitats within an estuary. Moreover, it is suspected that essential nursery habitat(s) of red drum vary ontogenetically (Bacheler et

al., 2009) and among estuarine systems (Stunz et al., 2002a). The purpose of this study was to examine the influence of biotic and abiotic factors on the distribution and abundance of juvenile red drum for three estuarine systems (Galveston, Aransas-Corpus Christi, and Laguna Madre) that differ in benthic habitat composition, hydrology, and physicochemical conditions. Furthermore, we explore these relationships across two life stages in the first year of life that have been described as potential bottlenecks in recruitment success of marine fishes, newly settled and overwintering (Hurst, 2007; Johnson, 2007).

Methods

The Texas coastline in the northwestern Gulf of Mexico is comprised of a series of estuaries along a latitudinal gradient from north to south, which vary in salinity, temperature, freshwater input, and benthic habitat coverage. Salinity increases from north to south, with estuaries in the north characterized by higher freshwater inflow and lower salinities, while estuaries in the south receive very little freshwater input with many considered negative estuaries that are often hypersaline (Tolan, 2007). Areal coverage of both seagrass and black mangrove (*Avicennia germinans*) increases from north to south as well (Sherrod and McMillan, 1981, Addair et al., 1994). Given this latitudinal variation in environmental conditions, we chose three estuarine systems in different locations of the Texas coast to examine variability in fish-habitat relationships for juvenile red drum: the Trinity-San Jacinto Estuary (referred to from hereafter as Galveston Bay) on the north coast, Mission-Aransas/Nueces Estuary (referred to

hereafter as Aransas-Corpus Bay) on the middle coast, and the Lower Laguna Madre (referred to from hereafter as Laguna Madre) on the southern coast (Figure 13). In addition differences in habitat availability and hydrology, these three estuaries also receive varying degrees of anthropogenic pressure, as Galveston Bay is adjacent to and receives effluent from the major metropolitan area of Houston (population > 2 million in city limits; U.S. Census Bureau, 2014). In contrast, Aransas-Corpus Bay is bordered to the southwest by the city of Corpus Christi (population > 300,000), while the Laguna Madre is largely undeveloped with the exception of the smaller city of Brownsville (population~175,000) at the southwestern tip of the estuary.

Juvenile red drum were collected as part of the Texas Parks and Wildlife Department (TPWD) long-term monthly bag seine surveys conducted from 1977-2014. In the current study, we limited catch data to a 15-year period from 2000-2014. Bag seine surveys were conducted based on a stratified, random sampling design, with each estuary divided into sampling grids (1' latitude by 1' longitude) and a fixed number of samples were taken per month (20 estuary⁻¹ month⁻¹). Bag seines (18 x 1.8 m, with 13 mm mesh in cod end) were deployed in shallow habitats (< 2 m) and pulled parallel to shore for approximately 15 m following methods described by Martinez-Andrade et al. (2005). This particular sampling gear targets juvenile red drum and is not particularly effective for larger more mobile individuals (age 1+), thus all individuals captured were presumed to be juveniles. Juvenile red drum catch data were partitioned into two life stages for modeling purposes. Newly settled red drum were defined here as individuals captured from October through December, which corresponds with documented

settlement patterns of the species (Rooker et al., 1998b), while early juvenile red drum were defined as individuals captured from January through March, corresponding to the first ‘overwintering’ period.

Environmental variables were used to investigate the influence physicochemical processes and habitat on red drum distribution and abundance in each estuary. Mean depth, dissolved oxygen (mg L^{-1}), salinity, water temperature ($^{\circ}\text{C}$), turbidity, as well as sampling date and geolocation were recorded by TPWD at each site during sampling. Distance to both freshwater sources and tidal inlets were estimated to examine the influence of freshwater and saltwater inflow on juvenile red drum distribution and abundance. Distance to a particular feature was calculated with the shoreline as a barrier using the cost-distance function in ArcGIS 10.2. Benthic habitat coverage of a particular site was also classified as the areal coverage of a particular habitat (seagrass, oyster, or salt marsh) within a 300-m radius of a sampling location and was calculated using geospatial modelling environment (GME, Beyer 2012). Seagrass, mangrove, and oyster reef habitat layers were obtained from the National Oceanic Atmospheric Administration (NOAA) National Coastal Data Development Center. Marsh habitat was defined as “estuarine intertidal emergent persistent vegetation” within the habitat classification scheme from georeferenced National Wetlands Inventory maps from the United States Fish and Wildlife Service (FWS).

Generalized additive models (GAMs) were used to investigate the influence of environmental variables on newly settled and early juvenile red drum abundance for Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. Catch per unit effort (CPUE;

individuals per seine haul) at each station was modeled as a count variable. GAMs are non-parametric extensions of general linear models (GLM) that allow for non-linear relationships between predictor and response variables that are common to ecological data (Guisan et al., 2002). General GAM construction is given by the equation:

$$E[y] = g^{-1} \left(\beta_0 + \sum_k S_k(x_k) \right)$$

where $E[y]$ is equal to the expected value of the response variable (CPUE), g is the link function, β_0 is the intercept, x represents one of k predictor variables, and S_k is the smoothing function of the predictor variable, x_k . Negative binomial models with a logarithm link were fit with cubic regression splines using the *mgcv* library in R version 3.1.3 (Wood, 2006; R Core Team, 2015). Cubic regression splines were automatically penalized from a specified maximum degrees of freedom and the degree of smoothing selected by minimizing the Generalized Cross Validation (GCV) (Wood, 2011). In the current study, cubic splines were restricted to a maximum three degrees of freedom for all predictor variables to prevent overfitting (i.e. unrealistic ecological responses) (Cianelli et al., 2008; Sundblad et al., 2009).

Predictor variables influencing juvenile red drum CPUE were selected for final models using a manual backwards stepwise procedure based on minimizing the Akaike Information Criterion (AIC; Akaike, 1974), which measures goodness of fit, while accounting for model complexity (number of variables). Approximate significance of smoothed predictor variables (p-values) was used to guide backwards selection procedure, where variable with the highest p-value was removed first. When removal of

a predictor variable resulted in a reduced model with a lower AIC, this variable was excluded from analysis. Stepwise selection continued until removal of any of the remaining predictor variables resulted in an increase in model AIC. Non-significant terms retained in the final model were removed if model AIC was comparable (<1%) after removal (Rooper et al., 2012). Prior to variable selection, Spearman's ρ was used to test for collinearity between predictor variables. If Spearman's ρ was > 0.5 between two variables, each variable was tested alone in separate GAMs and the variable that indicated better model fit (lower AIC) was included in the initial model prior to backwards selection. In addition to AIC, overall model fit was assessed with percent deviance explained ($([\text{null deviance} - \text{residual deviance}] / \text{null deviance}) \times 100$). The relative influence of each predictor variable was assessed by removing each variable individually from the final model and comparing percent change in deviance explained and change in AIC.

Results

Overall, 8,395 juvenile red drum were collected in the three estuarine systems over the 15 year period analyzed. Mean length of newly settled red drum decreased with decreasing latitude (ANOVA; $P < 0.001$), with the largest individuals in Galveston Bay (48.8 ± 0.6 mm; mean \pm SE), followed by Aransas-Corpus Bay (44.9 ± 0.5 mm), and Laguna Madre (41.3 ± 0.6 mm) (Tukey's HSD; $P < 0.001$) (Table 3). Size variability among the estuaries was also observed for early juvenile red drum (ANOVA; $P < 0.001$) with greater mean lengths observed in Aransas-Corpus Bay (68.3 ± 0.6 mm) relative to

Galveston Bay (62.0 ± 0.9 mm) and Laguna Madre (61.8 ± 0.9 mm) (Tukey's HSD; $P < 0.001$), which were both similar (Tukey's HSD; $P = 0.984$). Mean CPUE for newly settled red drum was higher in Laguna Madre (0.94 ± 0.13 ; mean \pm SE) and Aransas-Corpus Bay (0.93 ± 0.14) than Galveston Bay (0.63 ± 0.07) (Table 3); however, differences were not statistically significant (ANOVA; $P > 0.05$). Similarly, CPUE for early juvenile red drum decreased from north to south (ANOVA; $P < 0.01$), with higher values observed in Laguna Madre (3.03 ± 1.00), relative to Aransas-Corpus Bay (1.00 ± 0.02) and Galveston Bay (0.88 ± 0.11) (Tukey's HSD; $P \leq 0.01$).

Intra- and inter-annual variability in CPUE of juvenile red drum was observed for all three estuarine systems. Annual CPUE for newly settled red drum ranged from 0.23 (2010) to 1.00 (2008) in Galveston Bay, from 0.05 (2011) to 2.60 (2014) in Aransas-Corpus Bay, and from 0.05 (2011) to 2.47 in Laguna Madre (2012) (Table 4). Newly settled red drum abundance peaked earlier in Galveston Bay, in November (0.84)/December (0.85), relative to Aransas-Corpus Bay (December; 1.68) and Laguna Madre (December; 1.55) (Figure 14). Annual CPUE was also variable during the early juvenile stage and ranged from 0.20 (2004) to 1.97 (2001) in Galveston Bay, from 0.13 (2013) to 2.17 (2005) in Aransas-Corpus Bay, and from 0.17 (2000) to 28.83 (2014) in Laguna Madre. In contrast, monthly CPUE of early juvenile red drum followed the opposite pattern of the newly settled stage, and peaked earlier in Aransas-Corpus Bay (February) and Laguna Madre (February) than in Galveston Bay (March).

Newly Settled Models

The final model for newly settled red drum in Galveston Bay included 9 variables with an AIC of 1672.6 and a percent deviance explained of 27.3% (Table 5). Retained variables with associated Δ AIC values were month (70.7), seagrass coverage (61.4), salinity (30.8), year (22.1), salt marsh coverage (17.2), and turbidity (13.7), depth (6.9), oyster coverage (5.8), and temperature (3.3). Similarly, Δ DE indicated that the four most influential predictor variables were month (5.8%) and seagrass coverage (4.8%), year (3.8%), and salinity (2.9%). Response plots indicated that CPUE of newly settled red drum was reduced at higher salinities (>25) and at greater depth (>0.6 m), but was positively related to temperature (greatest above 25°C) (Figure 15). CPUE of newly settled red drum was also influenced by benthic habitat structure, with abundance higher in areas of moderate marsh coverage (30-60%) and positively related to areal seagrass coverage (Figure 16). Finally, abundance of newly settled red drum was negatively related to oyster coverage and turbidity.

In contrast, the final model for newly settled red drum in Aransas-Corpus Bay included 10 variables with an AIC of 3285.4 and a percent deviance explained of 44% (Table 5). Comparison of Δ AIC among retained variables indicated that year (185.6), depth (105.0), month (64.7), seagrass coverage (63.4), distance to freshwater (62.4), salt marsh coverage (57.8), and temperature (48.8) were the most influential variables with turbidity (30.6), oyster coverage (17.9), and salinity (14.4) also contributing to the final model. Findings were similar using Δ DE values, and observed Δ DE values were highest for year (5.8%), depth (3.1%), month (1.9%), seagrass coverage (1.9%), and distance to

freshwater (1.9%). Response plots indicated that newly settled red drum in Aransas Corpus Bay were found in greater abundance in shallow to moderate depths (0.1–0.5 m) far from freshwater sources (> 10 km), with moderate temperature (15-25°C) and salinities above 10 (Figure 15). CPUE was also influenced by benthic habitat structure, and was higher in areas with low to moderate areal coverage of seagrass (20-50%) and moderate to high coverage of marsh habitat (30-70%) (Figure 16). In addition, red drum abundance was reduced in areas with greater turbidity (>100 NTU) and moderate to high oyster reef coverage (>25%), relative to other areas surveyed.

Lastly, the final model for newly settled red drum in Laguna Madre included 9 variables with an AIC of 1781.4 and a percent deviance explained of 42.1% (Table 5). Retained variables (Δ AIC) were year (119.9), distance to inlet (55.6), month (35.9), salinity (27.1), temperature (26.2), mangrove coverage (14.1), oyster coverage (10.3), turbidity (8.0), and distance to freshwater (7.4). Δ DE was in general agreement with the Δ AIC method, and indicated that year (8.8%), distance to inlet (3.4%), month (2.4%), salinity (1.9%), and temperature (1.9%) were the most influential variables on red drum abundance. Response plots indicated that CPUE of newly settled red drum was highest at moderate temperatures (15-25°C) and salinities (10-30) far from tidal inlets (> 15km) and relatively close to freshwater sources (< 5 km) (Figure 15). Abundance of newly settled red drum also decreased with greater areal coverage of both mangrove (> 15%) and oyster (> 10%) habitat (Figure 16).

Early Juvenile Models

The final model for early juvenile red drum in Galveston Bay included 9 variables with an AIC of 2069.5 and a percent deviance explained of 22.2% (Table 5). The most influential variables retained in the model (with Δ AIC values) were year (55.3), depth (55.2), temperature (43.5), seagrass coverage (32.7), distance to freshwater (10.0). The Δ DE for these variables ranged from 1.2-5.3%, and was less than 1% for the remaining 4 variables (salt marsh coverage, distance to inlet, month, and oyster coverage). Response plots indicated that early juvenile red drum were more abundant in areas near freshwater sources with warmer temperatures ($> 15^{\circ}\text{C}$) and shallow to moderate depths (< 0.6 m) (Figure 17). CPUE of early juvenile red drum was positively related to seagrass coverage and to a lesser extent oyster reef coverage, and greater abundance was observed in areas with low to moderate areal coverage of marsh habitat (10-50%), relative to other areas surveyed (Figure 18). A more complex relationship was observed with distance to tidal inlet, with greater CPUE of early juveniles at both moderate (10-25 km) and large distances ($> 55\text{km}$) from the tidal inlet.

In contrast, the final model for early juvenile red drum in Aransas-Corpus Bay included 11 variables with an AIC of 3958.9 and a percent deviance explained of 31.6% (Table 5). The most influential variables (with Δ AIC values) retained were year (360.3), salinity (96.0), temperature (92.2), seagrass coverage (62.9), distance to freshwater (44.6), month (43.0). Similarly, Δ DE values were highest for year (11.2%), salinity (2.9%), temperature (2.8%), and seagrass coverage (1.9%). Δ AIC was less than 40 for the remaining 5 variables (mangrove coverage, oyster coverage, marsh coverage, depth,

and turbidity) retained in the final model and Δ DE was less than or equal to 1.1.

Response plots from the final GAM indicated that early juvenile red drum in Aransas-Corpus Bay were most abundant in areas far from freshwater sources (> 25 km) with low to moderate seagrass coverage (10-40%) and moderate to high marsh coverage (30-75%); relative to other areas surveyed (Figure 17,18). CPUE of juvenile red drum was also positively related to salinity, temperature, and areal coverage of mangrove habitat, with higher abundance at temperatures above 15°C and salinities greater than 29. In addition, juvenile red drum abundance was negatively related to areal coverage of oyster reef habitat.

Lastly, the final model for early juvenile red drum in Laguna Madre included 11 variables with an AIC of 2240.2 and a percent deviance explained of 61% (Table 5). The most influential variables (with associated delta AIC) retained in the final model included year (413.6), depth (153.8), seagrass coverage (76.4), month (53.4), marsh coverage (32.8), and salinity (29.9), with distance to inlet (18.7), temperature (11.7), turbidity (11.7), oyster coverage (11.6), and mangrove cover (7.8) also contributing. The most influential variables according to Δ DE were similar, with the highest values observed for year (14.2%), depth (5%), seagrass coverage (2.4%), and salt marsh (1.1%). Response plots indicated that early juvenile red drum in Laguna Madre were most abundant in shallow to moderate depths (0.2 - 0.8m) far from tidal inlets (> 15 km) (Figure 17). CPUE was highest in areas with low areal coverage of seagrass (< 20%) and was reduced in areas of high seagrass coverage (>60%) (Figure 18). Early juvenile abundance was greatest at temperatures between 18-24°C, and was positively related to

salinity. In addition, abundance was negatively related to mangrove coverage, and was lower in areas with greater areal coverage of salt marsh (> 20%) and oyster reef (> 10%).

Discussion

Intra-annual variability in abundance of juvenile fishes is often reflective of the timing of recruitment to the nursery (Rooker et al., 1998b). Peak abundance of newly settled red drum occurred earlier in Galveston Bay (November-December) than the two southern estuaries (December), suggesting that recruitment to estuarine nurseries may be staggered from north to south along the Texas coast. Red drum spawning is temperature dependent (Wilson and Nieland, 1994; Lowerre-Barbieri et al., 2008) and is estimated to occur when coastal temperatures begin to drop from 27-29 to 24-25°C, as both hatching success and larval survival is optimal at about 25°C (Holt et al., 1981; Stewart and Scharf, 2008). This typically corresponds to a spawning season that can begin as early as late August and run through October (Wilson and Nieland, 1994; Rooker and Holt, 1997; Lowerre-Barbieri et al., 2008). Although we did not obtain coastal temperatures for the current study, estuarine temperature varied by 1.5 °C between each estuary along the latitudinal gradient during the study (lowest temperatures in Galveston Bay), suggesting that the optimal temperature range for spawning likely occurred earlier in Galveston Bay. Our finding that red drum mean length during the newly settled stage decreased with latitude (from 48 mm in Galveston Bay to 41 in Laguna Madre) despite the fact that growth rates are known to be higher in the southern estuaries (Scharf et al., 2000), is also indicative of a north to south gradient for the onset of spawning with an

earlier spawning period and hence longer growing season in Galveston Bay. Latitudinal variation in spawning period and growth are known to occur in estuarine fishes, and are especially common in fall spawning fishes to maximize growth in the warmer waters prior to winter as overwinter mortality is often size-selective (Conover, 1992; Sogard et al, 1997; Hurst, 2007). Field experiments indicate that red drum growth decreases dramatically as temperatures decline in late fall and winter (Lanier and Scharf, 2007), and therefore an earlier onset to spawning in Galveston Bay would be advantageous as it would allow for an extended growing period prior to winter to maximize survival (Anderson and Scharf, 2014).

Inter-annual variability in the abundance of juvenile fishes is often high in marine and estuarine systems (Fogarty et al., 1991, Myers et al., 1997), and year was among the most influential variables in models for newly settled red drum. Similar to our results, previous time series analyses of red drum recruitment over multi-decadal scales along the Texas coast documented high inter-annual variability in the abundance of newly settled red drum in estuarine habitats (Scharf, 2000). Recruitment of pelagic larvae to benthic juvenile habitat is dependent on physical factors (i.e. currents, wind, freshwater inflow) affecting larval transport into the estuary (Brown et al., 2004; 2005) as well as biotic factors such as spawning success and behavior-mediated traits that affect survival (Fuiman and Cowan, 2003). Thus, while the availability of suitable juvenile habitat is likely to influence the abundance of settlers and early juveniles, variability in physical and biotic factors influencing larval supply is often a much stronger scalar of recruitment variability (Brown et al., 2005). High interannual

variability in red drum abundance was also observed during the early juvenile stage; however, there was little to no correlation in abundance between the two life stages in any of the estuaries. This may indicate that the early juvenile stage represents an important recruitment bottleneck and that year class strength may be determined by survival through the first winter of life rather than at settlement (Hurst et al., 2007). Overwinter mortality is known to be an important determinant of year class strength in temperate estuarine fishes (Hurst and Conover, 1998) and has been suggested previously as a likely source of mortality in early juvenile red drum (Stewart and Scharf, 2008; Anderson and Scharf, 2014). Alternatively, high overall mean abundance of early juveniles across all three estuaries could indicate low overwinter mortality; however, this trend was variable across years, with higher abundance in the newly settled stage in some years, suggesting that high overwinter mortality for early juveniles is likely episodic (Stewart and Scharf, 2008).

Temperature is known to be an important factor influencing both growth and survival of juvenile fishes and was retained in five of the six models (exception early juveniles in Laguna Madre). Despite differences in mean temperatures among the estuaries, similar patterns in abundance were observed across the three systems for each life stage, with both stages of red drum most abundant between 15-25°C and rarely found below 15°C during the early juvenile stage. Similar to our findings, previous large-scale studies in North Carolina described a peak in abundance between 15-25°C for juvenile red drum in estuarine habitats (Bacheler et al., 2008), suggesting this temperature range may represent an optimal range of available temperatures for red

drum during the newly settled and early juvenile stages. While laboratory trials indicate that the minimum cold tolerance of red drum can range from 2-5°C (Anderson and Scharf, 2014), other studies have shown that winter growth is negligible or even negative at temperatures below 15°C (Lanier and Scharf, 2007). Therefore, red drum may preferentially select habitats with temperatures greater than 15°C to optimize growth and survival during fall and winter. Abundance of newly settled drum was higher at temperatures greater than 25°C in Galveston Bay, which appears to reflect the aforementioned earlier onset of spawning and hence an earlier settlement period relative to the two southern estuaries. Therefore decreased abundance of red drum at temperatures above 25°C in Aransas-Corpus Bay and Laguna Madre may be more reflective of the later timing of recruitment in these estuaries rather than an aversion to warmer temperatures, as peak abundance occurred in the coldest month of the newly settled period (December) and those areas with temperatures greater than 25°C may have not been available.

Salinity often influences the distribution of estuarine organisms (Kimmerer, 2002), and response to salinity differed among life stages and estuaries in the current study. Newly settled red drum were generally most abundant in mesohaline conditions (near 20) in all three estuaries and low to moderate salinity (0 - 25) in Galveston Bay. While the isosmotic salinity for red drum is 10-11, this species is able to tolerate a wide range of salinities from marine to freshwater, and field experiments with juvenile red drum suggest that growth is optimized at mesohaline conditions (Lanier and Scharf, 2007). Laboratory trials demonstrated that the metabolic costs of osmoregulation for

juvenile red drum are minimalized at moderate salinities (~20), increasing the metabolic scope for growth (Wakeman and Wohlschlag, 1983; Lanier and Scharf, 2007).

Therefore, because of the importance of fast growth in maximizing size prior to winter (Sogard et al., 1997), it may be advantageous for newly settled red drum to recruit to mesohaline nurseries to optimize growth potential. Conversely, the abundance of early juvenile red drum was positively related to salinity in both Aransas-Corpus Bay and Laguna Madre, with high abundances occurring at near marine salinities (30+). These two estuaries receive very little freshwater input relative to Galveston Bay, and Laguna Madre is considered a negative estuary (Tolan, 2007); therefore, the majority of available juvenile habitat within both Aransas-Corpus Bay and Laguna Madre occurs in higher salinity waters, which could explain the increase in abundance with salinity.

Estuarine ecosystems are uniquely affected by both marine and freshwater inputs, and thus proximity to tidal passes and/or freshwater sources can additionally influence the value of nursery habitats (Froeschke et al., 2010; Furey and Rooker, 2013). Distance to freshwater sources was retained in 4 of the 6 models, but the proximity of newly settled and early juvenile red drum to freshwater sources differed among estuarine systems. Abundance of newly settled red drum was greater near freshwater input in Laguna Madre, while early juvenile red drum were generally less abundant near freshwater sources in Aransas-Corpus Bay. Because the Laguna Madre is often hypersaline, submerged aquatic vegetation is more widely distributed throughout the bay (Sheridan and Minello, 2003). Therefore, areas near freshwater inputs may represent important nursery areas that provide mesohaline salinities that are favorable for growth

and survival (Lanier and Scharf, 2007). However, submerged aquatic vegetation is less prevalent in the upper reaches of Aransas-Corpus Bay, suggesting that newly settled red drum may more likely recruit to more suitable benthic habitat in the lower to mid estuary. Increased abundance of overwintering red drum near freshwater inputs in Galveston Bay may be reflective of a thermal response, as estuarine organisms are known to seek thermal refuge near warmer freshwater sources during winter (Akin et al., 2003, Callihan et al., 2013). The fact that a similar pattern was not observed in Aransas-Corpus Bay and Laguna Madre may be due to colder overwinter temperatures in Galveston Bay (mean ~ 16°C) relative to the other two systems. Because adult red drum are known to spawn in coastal waters, it might be expected that the abundance of newly settled individuals would be higher near tidal inlets where larvae first enter the estuary. Instead, our models indicated that red drum abundance was typically unrelated to proximity to tidal inlets or increased with increasing distance from tidal inlets. This could be due in part to the lack of optimal benthic habitat near tidal inlets, but may also be related to the preference for mesohaline conditions that are more prevalent in the mid estuary. In contrast, previous studies have indicated that the abundance of juvenile red drum in Aransas-Corpus Bay is closely related to distance to tidal inlet, and although distance to tidal inlet was not retained in either Aransas-Corpus model because of collinearity (negative correlation) with distance to freshwater, the finding that red drum abundance increased at greater distances from freshwater in this estuary appears to support this notion.

Benthic habitat structure often influences the distribution and abundance of estuarine organisms (Boström et al., 2011; Pittman and Brown, 2011). Submerged aquatic vegetation such as seagrass beds are known to serve as important nursery habitat for juvenile fishes and invertebrates, and they have been shown to enhance growth and survival of juvenile red drum (Rooker et al., 1998a; Stunz et al., 2002b). Seagrass coverage was among the most important predictors of red drum abundance in our models; however, the relationship between seagrass coverage and red drum abundance was estuary specific. This is not surprising given that the availability of seagrass varies along a latitudinal gradient on the Texas coast. Seagrass coverage is limited in Galveston Bay but increases from north to south by greater than 3 orders of magnitude from Galveston Bay to Laguna Madre. In the current study, we found that red drum abundance was associated with greater seagrass coverage in Galveston Bay, moderate coverage in Aransas-Corpus Bay, and lower coverage in Laguna Madre. The observed differences may be reflective of the preference for patchy seagrass habitats by juvenile red drum, as ecotones at the edges of seagrass beds often provide greater foraging opportunities while still affording protection from predators (Holt et al., 1983; Bologna and Heck, 2002). Previous research in the northern Gulf of Mexico has shown that juvenile red drum abundance is typically higher in patchy seagrass beds relative to homogenous beds (Holt et al., 1983), a notion that is also supported by recent telemetry studies with juvenile red drum (Dance and Rooker, in press). Therefore, in estuaries where seagrass is ubiquitous and present in large homogenous stands such as in Laguna Madre, areas with reduced seagrass coverage may provide more heterogeneous habitat

preferred by red drum. Conversely, our finding that juvenile red drum abundance increased with coverage of seagrass in Galveston Bay, suggests that the influence of seagrass on red drum distribution is likely stronger in estuaries where seagrass is limiting.

In addition to seagrass, other estuarine habitats such as salt marsh, oyster reef, and mangrove are frequently cited as important early life habitats for juvenile fishes and invertebrates (Stunz et al., 2002; Minello et al., 2003; Mumby et al., 2004). Salt marsh coverage was retained in 5 of the 6 final models, and red drum abundance was generally higher in areas with low to moderate coverage of salt marsh habitat. In temperate and subtropical regions, salt marsh habitats are known to serve as nursery habitats for fishes and invertebrates (Minello et al., 2003), and previous studies suggest that salt marshes act as an alternative habitat for red drum when seagrass is limited (Stunz and Minello, 2001; Stunz et al., 2002b). Fish abundance is known to be highest in areas within 1 meter on either side of the salt marsh edge (Minello et al., 2003) relative to the marsh interior; therefore, lower abundance might be expected in areas with high marsh coverage. In contrast, areas of moderate salt marsh coverage likely corresponded to areas with greater edge habitat that is more suitable for juvenile red drum. Moreover, the finding that red drum preferred areas of low to moderate coverage of both seagrass and salt marsh in Aransas-Corpus Bay and Laguna Madre suggests that areas containing mixtures of habitat types (i.e. seagrass adjacent to salt marsh) may enhance nursery habitat value (Levin and Stunz, 2005; Baillie et al., 2014). Oyster reef coverage was retained in all models, but was not among the most important variables in any, as

juvenile red drum abundance was generally higher in areas where oyster reef habitat was absent or less prevalent. Similar findings have been described in other studies (Stunz et al., 2002a; Furey and Rooker, 2013), and it may be that oyster reefs do not offer the forage resources that submerged aquatic vegetation does as growth of juvenile red drum inhabiting oyster reefs has been shown to be reduced relative to other habitats (Stunz et al., 2002b). Alternatively, oyster reefs are known to hold high densities of larger estuarine predators (Robillard et al., 2010), which may increase predation risk and reduce the nursery value of this habitat for juvenile fishes. In recent years, mangrove habitats have expanded northward in the northwestern Gulf of Mexico, and have become increasingly prevalent in Laguna Madre and Aransas-Corpus Bay (Armitage et al., 2015). In the current study, abundance of juvenile red drum was greater in areas with mangrove coverage in Aransas-Corpus Bay, while it was typically reduced in areas with higher mangrove coverage in Laguna Madre. Relatively little is known about the effects of mangrove expansion on the distribution and abundance of estuarine fauna in the Gulf of Mexico, and thus the reduced use of mangroves in Laguna Madre may be related to competition from tropical fauna that are typically associated with mangroves (Gericke et al., 2014) and are more prevalent in Laguna Madre than Aransas-Corpus Bay.

Here, we demonstrate that the suitability of nursery habitat for newly settled and early juvenile stage red drum is spatially and temporally dynamic, regulated by complex relationships between environmental factors (biotic and abiotic) that can vary both ontogenetically and regionally. While fish-habitat relationships were frequently similar across the three estuaries, the relative importance of abiotic and biotic factors to juvenile

red drum distribution and abundance differed, suggesting that habitat quality within each life stage may be determined by variables that have the greatest impact on survival in a particular estuary. Likewise, our results indicate that seasonal shifts in abiotic conditions between the newly settled and early juvenile stages can alter fish-habitat relationships, presenting tradeoffs between the shelter provided by benthic habitat coverage and optimal abiotic conditions (e.g. temperature and salinity) that can improve growth and/or fitness. This study clearly shows that fish-habitat relationships for red drum are life stage-, time- and estuary-specific, suggesting that habitat suitability models for other estuarine taxa may be similarly spatio-temporally explicit. As a result, such models may not be applicable across multiple regions or life stages as the composition and location of critical nursery habitats are likely to also be estuary-specific.

CHAPTER V

SUMMARY AND CONCLUSIONS

Understanding the relative value of nursery habitats is important to the conservation of coastal fisheries. The three studies in this dissertation utilized complementary approaches to address gaps in our knowledge of nursery habitat value for both juvenile red drum and southern flounder within estuarine seascapes. Results of this study demonstrate that habitat use and movement patterns are both spatially and temporally dynamic within and among estuarine nursery areas.

In Chapter II, I used an experimental approach to test the influence of three biotic factors on the detection range of acoustic transmitters in estuarine environments. The three experiments included: internal versus external placement of the transmitter on a model finfish species, red drum; attachment of a transmitter on an animal host (red drum) versus a fixed object; and species comparison between internally tagged red drum and southern flounder. Significant differences in detection probability were observed between internally and externally placed transmitters as well as between transmitters attached to an animal host and those attached to a fixed line, while no effect was observed between the two species tested. External transmitters were detected substantially more than corresponding internal transmitters in red drum, and outperformed internal transmitters by 2-7 fold at distances > 100m. Similarly, detection probability declined more quickly as a function of distance for transmitters attached to red drum relative to transmitters attached to a fixed line, with greater differences

observed at distances $> 300\text{m}$. Findings from this study challenge commonly held assumptions in acoustic telemetry research and suggest that traditional range testing methods are likely to overestimate detection ranges of tagged animals *in situ*. Moreover, accounting for the influence of transmitter placement will enhance study design in acoustic telemetry research and ultimately improve detection efficiency and data interpretation in animal movement studies.

Acoustic telemetry was used in Chapter III to examine habitat- and bay-scale connectivity for co-occurring juvenile fishes, red drum and southern flounder, at two spatial scales (habitat and bay) in a model estuarine seascape. Both species exhibited a preference for edge habitat and seagrass beds at the habitat scale; however, rates of movement within habitats varied between species. Southern flounder movement increased with decreasing habitat complexity (seagrass to bare sand) and increasing temperature, while red drum rate of movement was not significantly affected by environmental factors at the habitat scale, which likely reflected different foraging strategies (i.e. ambush vs. active) used by the two species. 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 for southern flounder was greatest on days with narrow tidal ranges and higher temperatures, while the probability of bay-scale movement for red drum increased in response to decreasing salinity and lower temperatures. Species-specific variation in movement patterns within

and across habitat types observed here at both the habitat and bay scale suggest that sympatric species employ different strategies to partition resources within estuarine nursery areas and highlight the importance of multi-species assessments to improving our understanding of habitat value and ecosystem function.

A generalized additive model (GAM) framework was used in Chapter IV to characterize and contrast stage-specific habitat relationships for juvenile red drum in three estuaries (Galveston Bay, Aransas-Corpus Bay, and Laguna Madre) along a latitudinal gradient in the northwestern Gulf of Mexico. High inter- and intra-annual variability in abundance of juvenile red drum was observed in each of the three estuaries, with inter-annual variability highest in Laguna Madre where habitat is more homogeneous, and intra-annual variability highest in Galveston Bay where physicochemical conditions were more variable. In addition to temporal variability, my findings indicate that the suitability of nursery habitat for newly settled and early juvenile stage red drum is spatially dynamic and driven by complex interactions among biotic and abiotic factors, which can vary both ontogenetically and regionally. Although fish-habitat relationships were often similar across the three estuaries, the relative importance of abiotic and biotic factors to juvenile red drum distribution and abundance varied, suggesting that habitat quality within each life stage may be determined by variables that have the greatest impact on survival within a particular estuary. Similarly, results indicate that seasonal shifts in abiotic conditions between the newly settled and early juvenile stages can alter fish-habitat relationships. This study clearly shows that fish-habitat relationships for red drum are life stage-, time- and estuary-specific.

Therefore, habitat suitability models may not be applicable across multiple regions or life stages as the composition and location of critical nursery habitats are likely to vary regionally.

The results of this research have several implications for the management of coastal fisheries in Texas and the northern Gulf of Mexico. The use of acoustic telemetry to monitor coastal movement and estuarine-coastal connectivity is becoming increasingly popular within the region, as such information is needed to improve management strategies of valuable fisheries in Texas (i.e. red drum, southern flounder, spotted seatrout). The finding that detection efficiency of acoustic transmitters can be greatly reduced by intracoelomic implantation of the transmitter will benefit the planning and deployment of acoustic arrays in Texas and improve future movement studies along the Gulf coast. Likewise, Texas estuaries face growing anthropogenic pressure that is contributing to habitat loss, increasing the need to prioritize the conservation of important nursery areas for many of the state's most economically valuable fisheries. This study demonstrates that sympatric species utilize estuarine seascapes differently, suggesting that approaches that account for differences in habitat use among managed species may be required to identify the seascapes needed to sustain coastal fisheries in Texas. Lastly, results from this study highlight the need to incorporate spatial and temporal information on habitat use into fisheries management plans to conserve the suite of habitats used by estuarine-dependent fish to complete their life cycle. This is especially important in a state such as Texas, where several estuaries along a latitudinal gradient are managed under statewide regulations. Because fish-habitat relationships

varied both regionally and ontogenetically, it is likely that similar results might be expected for other important estuarine species. As a result, a single definition of “high quality” juvenile habitat may not be applicable across the entire state and habitats may need to be prioritized differently in each region to ensure that our fisheries are sustainably managed.

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APPENDIX A

TABLES

Table 1. Mean difference (\pm SE) in detection probability as a function of distance between paired samples for three experiments testing biotic factors influencing detection efficiency of acoustic transmitters: 1) Ext-Int (difference between paired external and internal transmitters on red drum), 2) Fix-RD (difference between transmitter attached to a fixed line and transmitter externally attached to a red drum), 3) SF-RD (difference between transmitters internally implanted in southern flounder and red drum). Asterisks represent significant differences (paired t-test; $P < 0.05$), while q-values represent p-values adjusted to control the false discovery rate (also set at 0.05). Effect size is given as Cohen's d (d), where the corresponding effect size magnitudes using the thresholds defined in Cohen (1992) are: negligible ($|d| < 0.2$), small ($0.2 < |d| < 0.5$), medium ($0.5 < |d| < 0.8$), large ($|d| > 0.8$). Large effect sizes are indicated with bold font. Experiment 3 was only conducted between 0 and 400 m.

Distance	Experiment 1			Experiment 2			Experiment 3		
	Ext-Int	q	d	Fix-RD	q	d	SF-RD	q	d
50m	0.06 (0.03)	0.11	1.33	0.00 (0.02)	0.81	-0.35	0.01 (0.01)	0.56	0.52
100m	0.35 (0.13)	0.07	1.68	0.01 (0.04)	0.81	0.29	0.11 (0.06)	0.56	0.79
150m	0.48 (0.13)*	0.03	2.64	0.04 (0.06)	0.32	1.55	0.13 (0.13)	0.71	0.49
200m	0.57 (0.09)*	0.02	3.14	0.14 (0.09)	0.32	1.74	0.06 (0.14)	0.98	0.16
250m	0.60 (0.14)*	0.03	2.34	0.17 (0.10)	0.34	1.64	0.00 (0.11)	0.98	0.01
300m	0.64 (0.11)*	0.02	3.19	0.23 (0.08)*	0.20	3.10	-0.01 (0.09)	0.98	-0.03
400m	0.51 (0.12)*	0.03	1.99	0.26 (0.15)	0.28	1.99	-0.04 (0.04)	0.71	-0.46
500m	0.50 (0.14)*	0.03	1.87	0.24 (0.12)*	0.20	1.62			
600m	0.31 (0.09)*	0.03	1.66	0.22 (0.11)	0.20	1.19			

Table 2. 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

Table 3. Summary of red drum catch data and associated abiotic variables of both the newly settled (October-December) and early juvenile (January-March) life stages in three estuaries from the northern Gulf of Mexico from 2000-2014. Estuaries sampled were Galveston Bay, Aransas-Corpus Bay, and Laguna Madre.

Newly Settled						
Surveys	Galveston		Aransas-Corpus		Laguna Madre	
	n = 900		n = 1800		n = 900	
	Mean	SD	Mean	SD	Mean	SD
CPUE	0.63	2.11	0.93	5.84	0.94	4.03
Length (mm)	48.83	14.33	44.86	15.63	41.33	16.40
Temp. (°C)	20.10	5.27	21.76	5.60	23.17	5.23
Salinity	18.99	8.81	24.85	10.48	30.33	8.70
DO	7.89	1.84	8.53	2.34	7.07	2.42
Turbidity	32.08	55.86	21.59	35.85	25.55	42.53
Depth	0.33	0.19	0.26	0.14	0.18	0.07
Dist. to Freshwater (m)	11188.55	7764.90	18634.13	10790.31	19894.49	13398.40
Dist. to Inlet (m)	21653.41	15259.96	28407.00	14759.69	20628.24	9278.21

Early Juvenile						
Surveys	Galveston		Aransas-Corpus		Laguna Madre	
	n = 900		n = 1800		n = 900	
	Mean	SD	Mean	SD	Mean	SD
CPUE	0.88	3.18	1.00	5.59	3.03	30.13
Length (mm)	61.98	25.27	68.32	23.21	61.77	27.66
Temp. (°C)	16.72	4.18	17.69	3.98	19.52	4.14
Salinity	17.73	8.74	24.02	8.35	31.53	7.21
DO	8.41	1.73	8.38	1.96	7.82	1.91
Turbidity	37.05	55.15	18.82	29.67	33.77	60.67
Depth	0.28	0.14	0.20	0.11	0.15	0.07
Dist. to Freshwater (m)	11553.62	7754.18	18590.75	11053.58	20440.86	13339.02
Dist. to Inlet (m)	21476.35	15980.43	28017.82	14879.78	20523.95	9294.51

Table 4. Mean annual abundance of juvenile red drum in Galveston Bay, Aransas-Corpus Bay, and Laguna Madre between 2000-2014 during both the newly settled (October-December) and early juvenile (January-March) life stages. Abundance is given as catch per unit effort (CPUE), which was number of juveniles per seine haul (~300m²).

Year	Newly Settled			Early Juvenile		
	Galveston	Aransas-Corpus	Laguna Madre	Galveston	Aransas-Corpus	Laguna Madre
2000	0.75	0.34	0.42	0.67	0.64	0.17
2001	0.88	1.46	0.45	1.97	1.39	1.82
2002	0.60	1.61	0.88	1.37	0.57	0.58
2003	0.63	0.40	0.90	0.38	1.09	0.65
2004	0.77	1.98	0.33	0.20	1.86	1.63
2005	0.70	1.29	0.87	0.77	2.17	0.48
2006	0.23	0.48	0.73	0.93	0.47	0.98
2007	0.80	1.47	2.07	0.98	0.46	0.23
2008	1.00	0.63	0.45	0.97	1.26	1.55
2009	0.28	0.18	0.08	0.52	0.49	2.85
2010	0.23	0.86	1.12	1.20	1.92	0.27
2011	0.68	0.05	0.05	0.48	0.93	2.78
2012	0.40	0.42	2.47	0.90	0.47	0.93
2013	0.85	0.16	1.03	1.52	0.13	1.68
2014	0.68	2.60	2.22	0.35	1.12	28.83

Table 5. Temporal and environmental variables retained in final generalized additive models (GAMs) for juvenile red drum in three estuaries in the northwestern Gulf of Mexico. Estuaries include Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. Model fit was assessed with Akaike's Information Criterion (AIC) and % deviance explained (DE). Relative importance of each predictor variable is given by the difference in AIC (Δ AIC) and DE (Δ DE) when this variable was removed from the final model.

Newly Settled						
Galveston			Aransas-Corpus		Laguna Madre	
AIC = 1672.6 DE = 27.2			AIC = 3285.4 DE = 44.0		AIC = 1781.4 DE = 42.1	
Variable	Δ AIC	Δ DE	Δ AIC	Δ DE	Δ AIC	Δ DE
Month	70.7	5.8	64.7	1.9	35.9	2.4
Year	22.2	3.8	185.6	5.8	119.9	8.8
Temp	3.3	0.4	48.8	1.6	26.2	1.9
Salinity	30.8	2.9	14.4	0.6	27.1	1.9
Turbidity	13.7	1.3	30.6	1.0	8.0	0.8
Tidal inlet					52.6	3.4
Freshwater			62.4	1.9	7.4	0.7
Salt marsh	17.2	1.4	57.8	1.8		
Seagrass	61.4	4.8	63.4	1.9		
Oyster	5.8	0.6	17.9	0.7	10.3	0.9
Mangrove					14.1	1.1
Depth	6.9	0.8	105.0	3.1		
Early Juvenile						
Galveston			Aransas-Corpus		Laguna Madre	
AIC = 2069.5 DE = 22.2			AIC = 3958.9 DE = 31.6		AIC = 2240.2 DE = 61.0	
Variable	Δ AIC	Δ DE	Δ AIC	Δ DE	Δ AIC	Δ DE
Month	0.3	0.3	42.9	1.3	53.4	1.8
Year	55.3	5.3	360.3	11.2	413.6	14.2
Temp	43.5	3.3	92.2	2.8	11.7	0.5
Salinity			96.0	2.9	29.9	1
Turbidity			4.5	0.3	11.7	0.5
Tidal inlet	3.7	0.7			18.7	0.6
Freshwater	10.0	1.2	44.6	1.4		
Salt marsh	10.0	0.9	18.5	0.7	32.8	1.1
Seagrass	32.7	2.6	62.9	1.9	76.4	2.4
Oyster	1.3	0.2	33.0	1.1	11.6	0.5
Mangrove			36.4	1.1	7.8	0.3
Depth	55.2	4.1	15.4	0.6	153.8	5

APPENDIX B

FIGURES

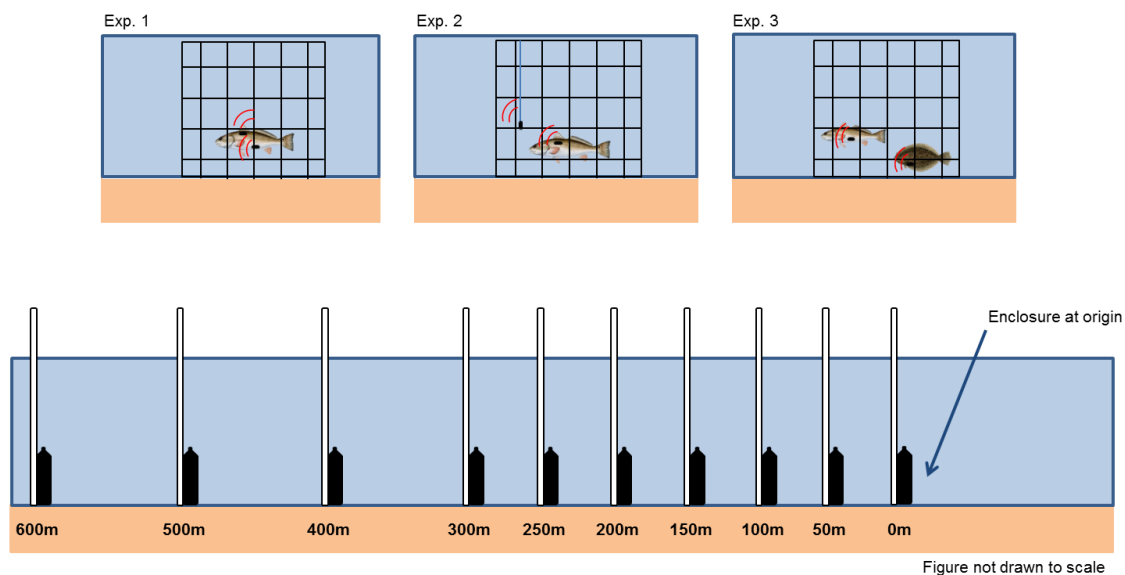


Figure 1. Schematic of experimental design, which consisted of a 1 m³ enclosure and a line of acoustic receivers secured to polyvinyl chloride (PVC) moorings at set distances from the enclosure (0, 50, 100, 150, 200, 250, 300, 400, 500, 600 m). In the first experiment (Exp. 1), red drum were simultaneously fitted with an internal and external transmitter. In the second experiment (Exp. 2), red drum were fitted with an external transmitter and a second transmitter was attached to a fixed monofilament line. In the third experiment (Exp. 3), both a red drum and southern flounder were fitted with an internal transmitter. Distances and sizes are not drawn to scale.

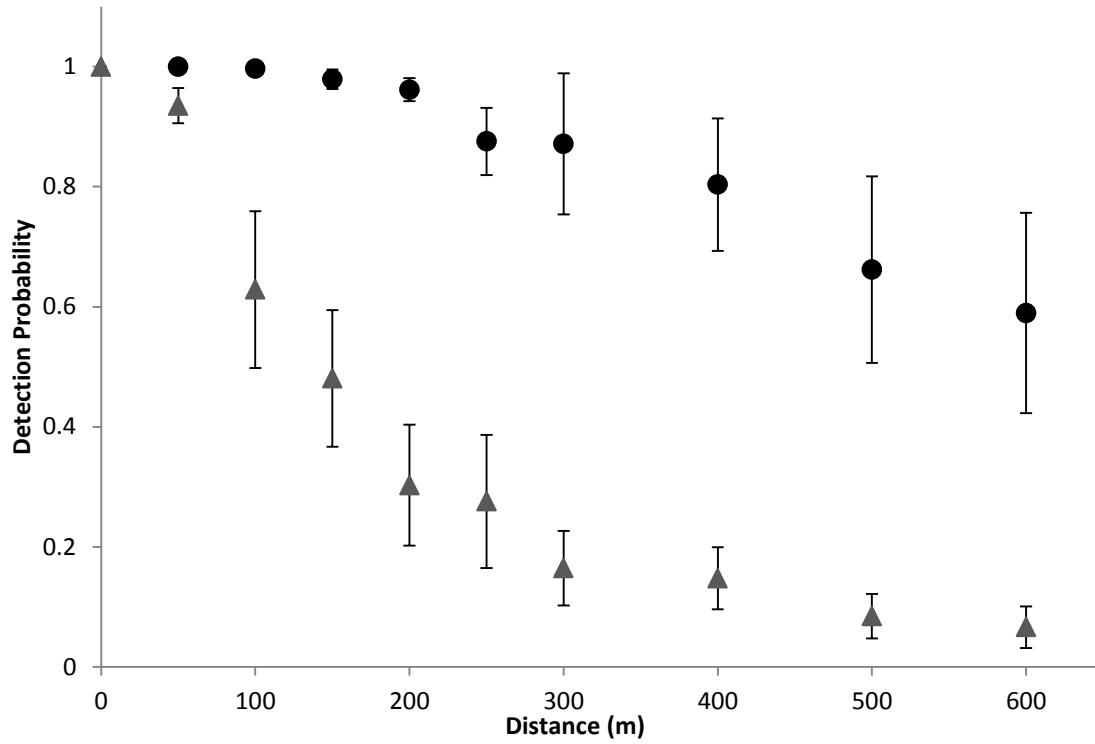


Figure 2. Mean detection probability as a function of distance for external (black circles) and internal (gray triangles) transmitters simultaneously attached to red drum. Error bars are ± 1 SE of the mean from five replicate trials.

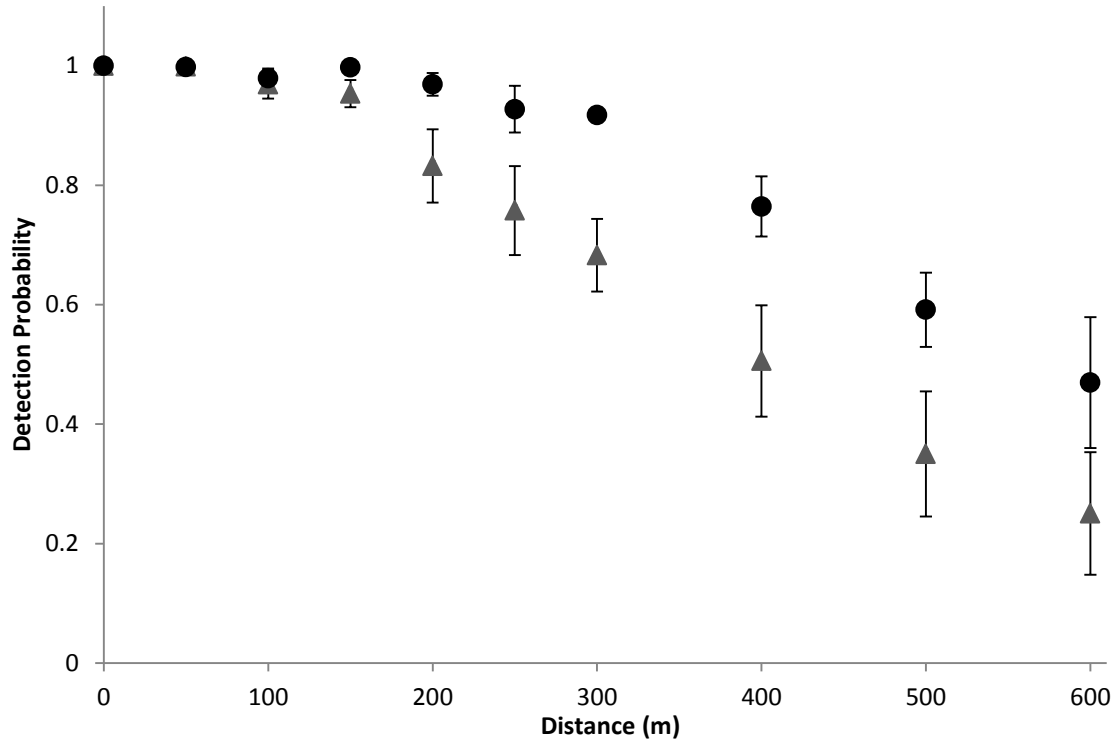


Figure 3. Mean detection probability as a function of distance for transmitters attached to a fixed line (black circles) and externally to red drum (gray triangles). Error bars are ± 1 SE of the mean from three replicate trials.

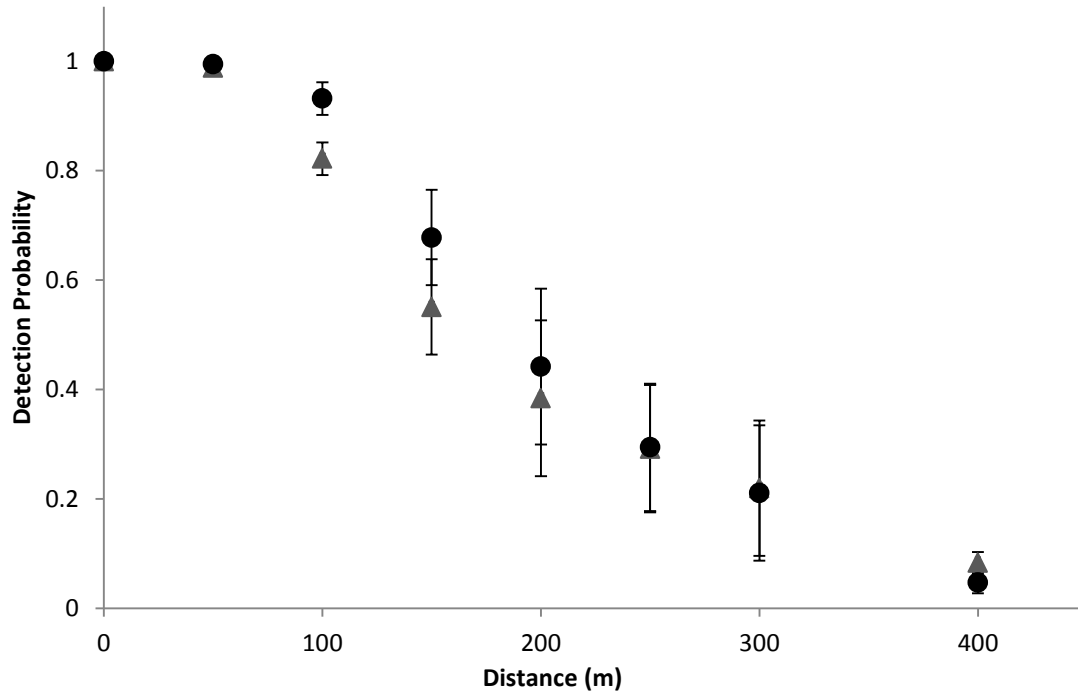


Figure 4. Mean detection probability as a function of distance for transmitters internally implanted in southern flounder (black circles) and red drum (gray triangles). Error bars are ± 1 SE of the mean from five replicate trials.

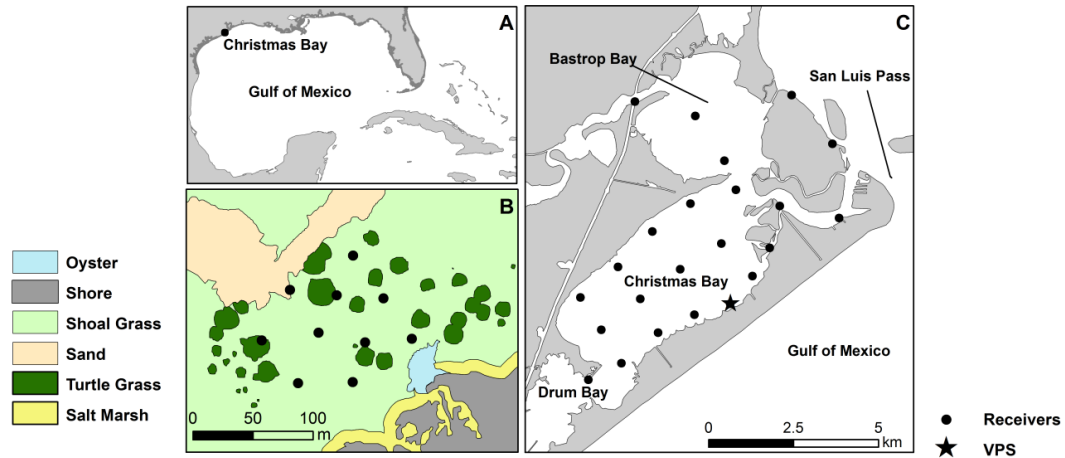
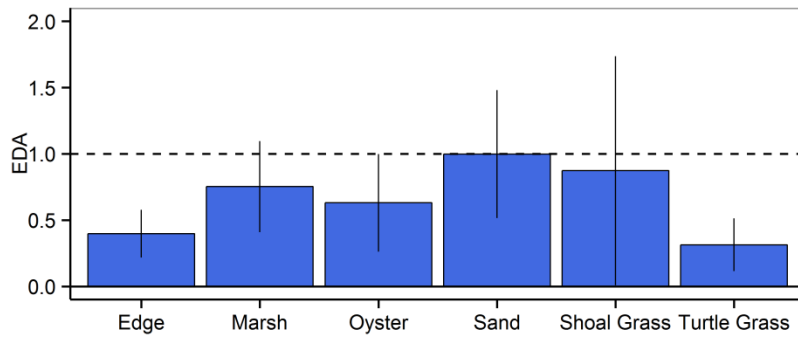


Figure 5. Map of study site. A) Location of Christmas Bay, Texas. B) Layout of Christmas Bay and surrounding sub-bays with location of the habitat-scale array and bay scale acoustic telemetry array. C) Layout of VPS acoustic telemetry array and spatial arrangement of habitats within the array.

Southern Flounder



Red Drum

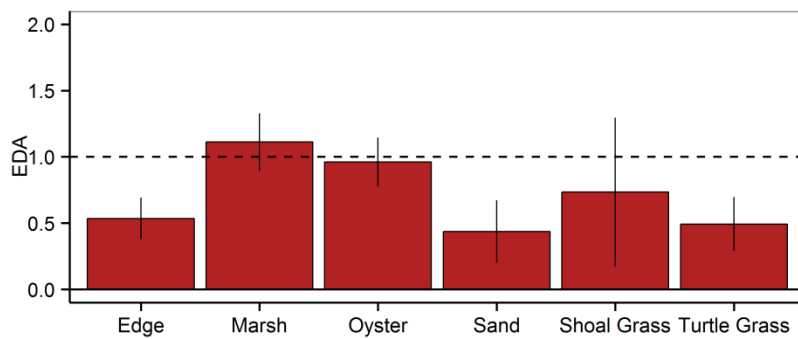


Figure 6. Mean EDA ratios demonstrating fine-scale habitat use for southern flounder and red drum. EDA ratios = 1 indicate habitat use is random, EDA ratios < 1 indicate relative preference, and EDA ratios > 1 indicate relative avoidance. Error bars are ± 1 standard deviation of the mean.

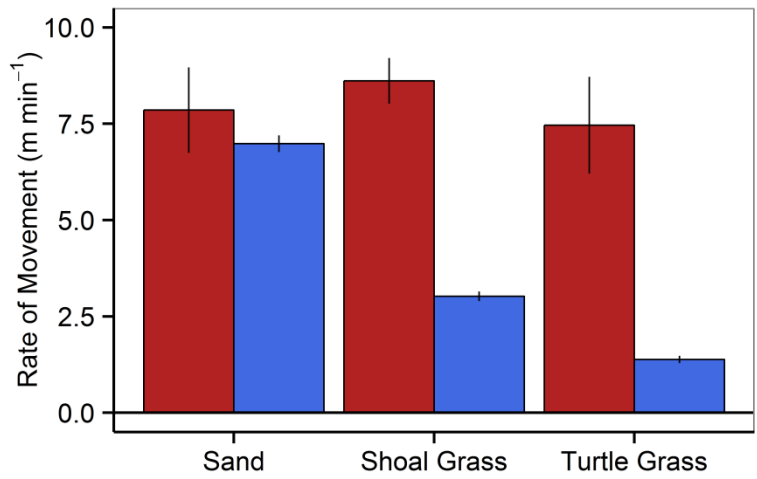


Figure 7. Fine-scale rates of movement (m/min) for southern flounder (blue) and red drum (red) across different estuarine habitat types. Habitat types include sand, shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*). Error bars represent \pm 1 standard error of the mean.

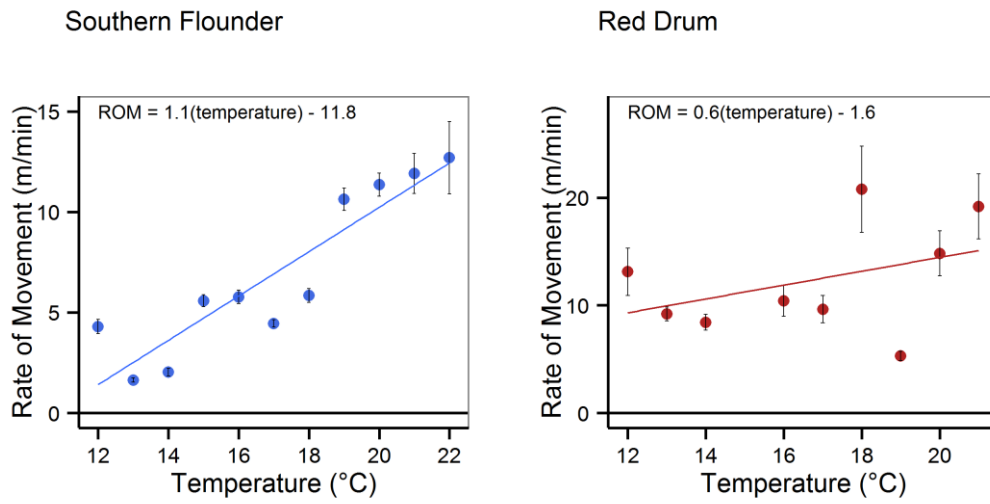


Figure 8. Linear regressions of mean rate of movement (ROM) against temperature for southern flounder (left, $r^2 = 0.83$) and red drum (right, $r^2 = 0.16$). Data points were derived from the species-specific mean rate of movement for 1° temperature bins. Error bars represent ± 1 SE of the mean.

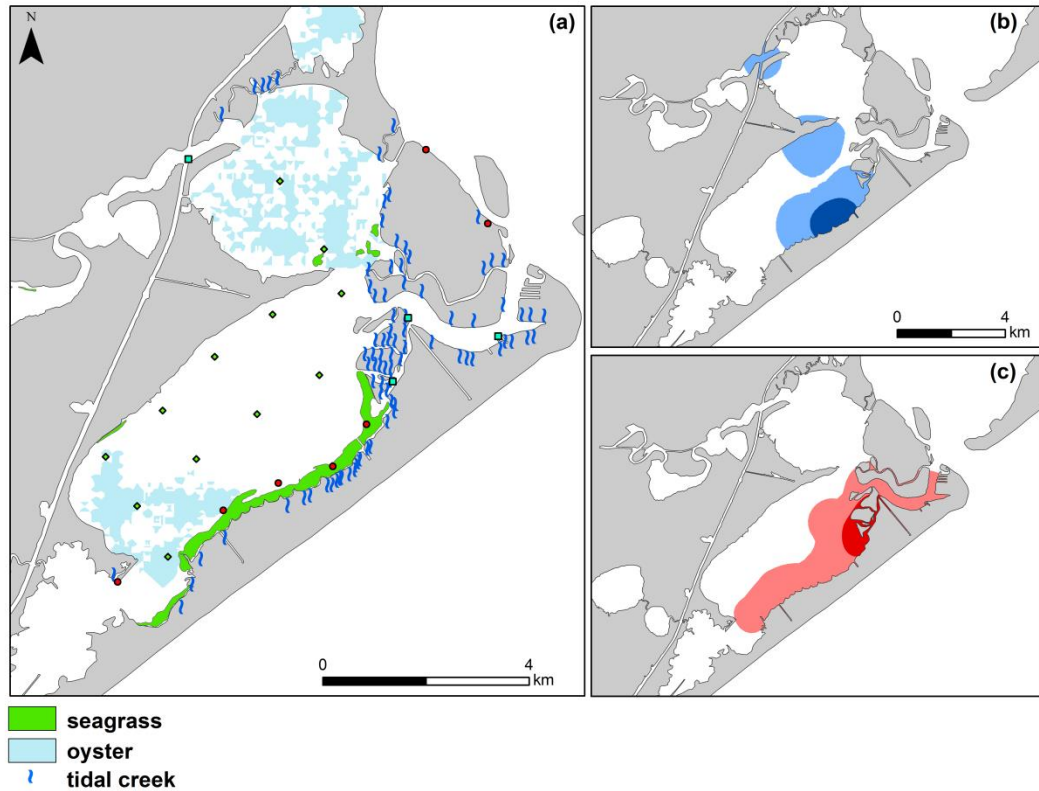


Figure 9. Maps of Christmas Bay showing: bay scale array with habitat coverage and acoustic receiver placement (a). Symbols represent receiver groupings based on similarity in multivariate seascape structure among the receiver listening areas and are defined as high (blue square), intermediate (red circle), and low (green diamond) marsh edge. 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).

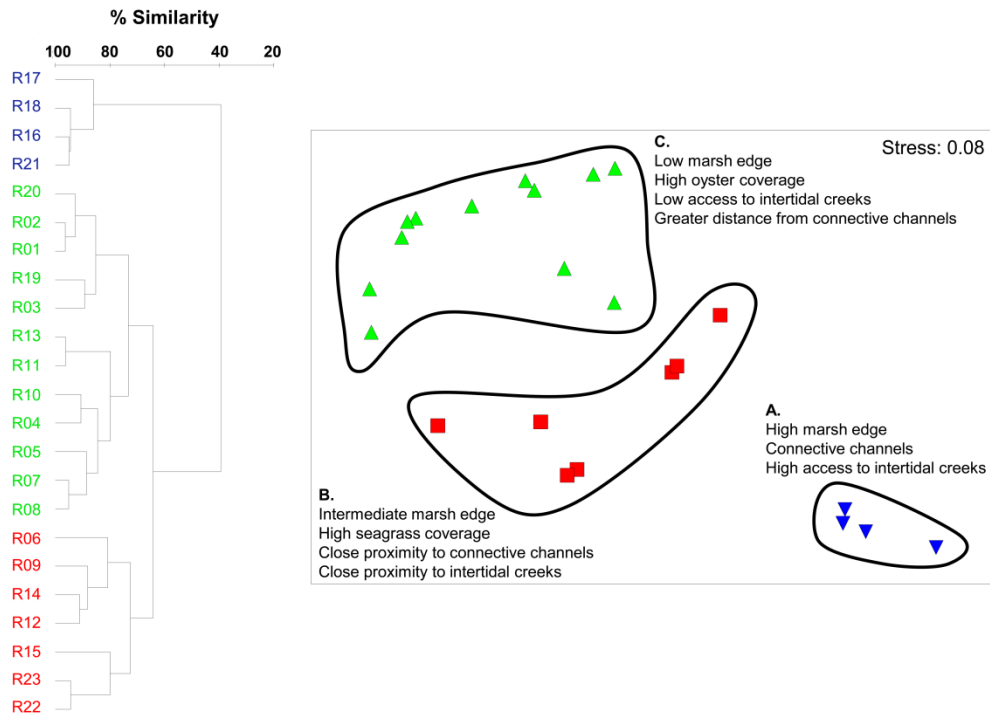


Figure 10. Hierarchical clustering and non-metric multidimensional scaling (nMDS) showing relative similarity in habitat composition (aerial seagrass coverage, aerial oyster coverage, and salt marsh edge) and connectivity (distance to connective channels, distance to intertidal creeks) among acoustic 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.

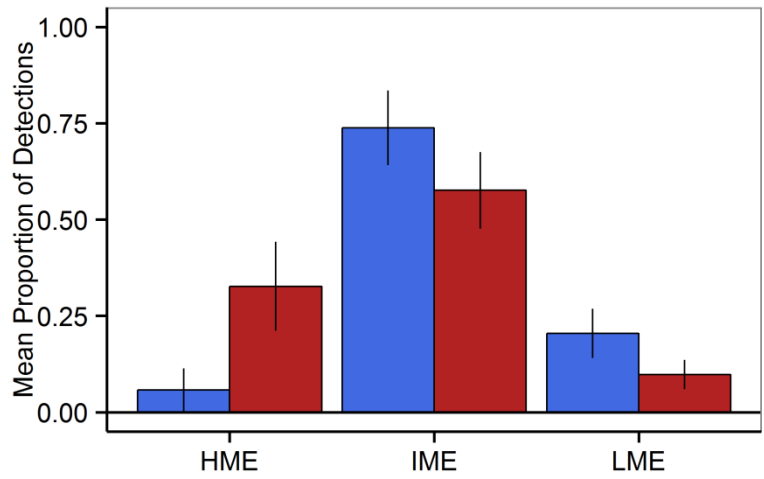


Figure 11. Mean proportion of detections of tagged southern flounder (blue, n = 8) and red drum (red, n = 14) at receivers located in each of three habitat groupings based on 70% similarity in multivariate seascape structure among receiver listening areas at the bay scale. Receiver groupings were defined 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.

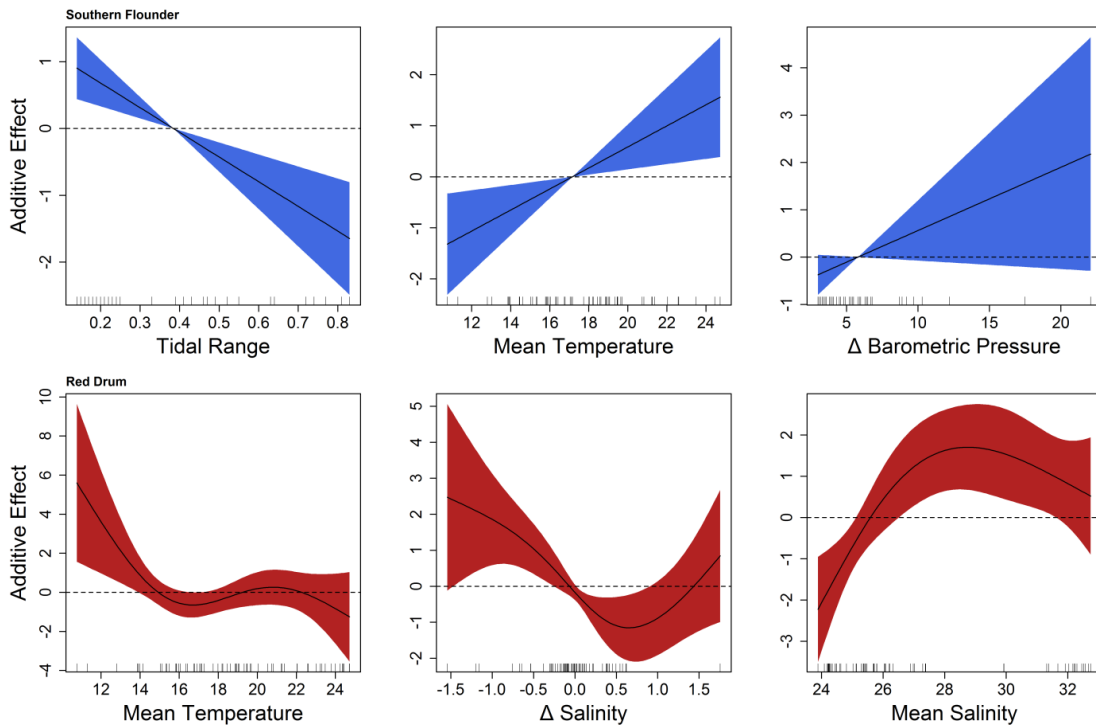


Figure 12. Response plots displaying the additive effect of environmental predictor variables on the probability of daily movement for juvenile southern flounder and red drum from final generalized additive models (GAMs) for each species. Retained variables for southern flounder GAMs include tidal range (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).

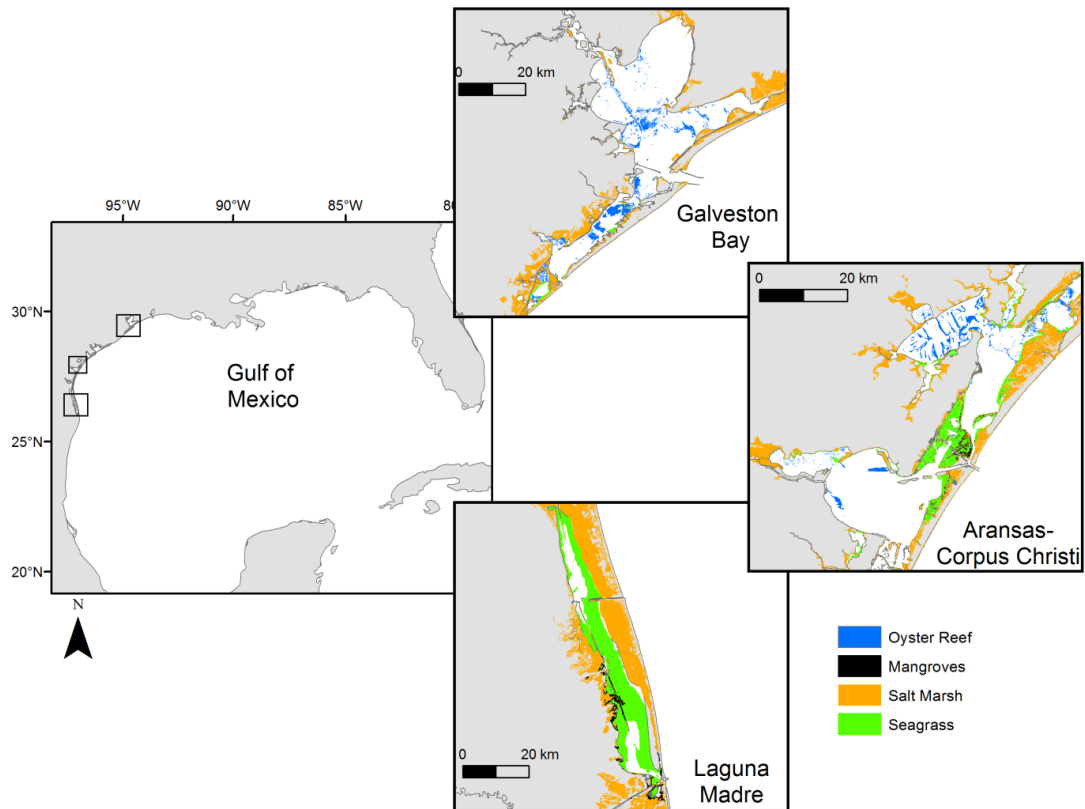


Figure 13. Study site and habitat distribution. Location of three estuarine systems located along a latitudinal gradient in the northwestern Gulf of Mexico: Galveston Bay, Aransas-Corpus Christi Bay, and Laguna Madre (left). Distribution of benthic habitat within Galveston Bay (upper right), Aransas-Corpus (middle right), and Laguna Madre (lower right).

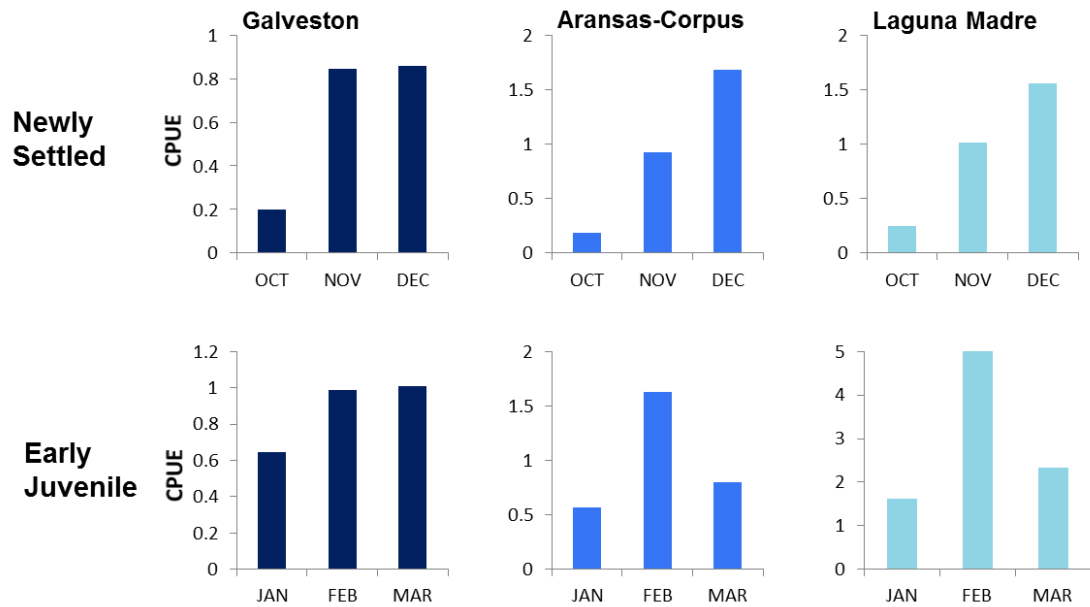


Figure 14. Plots of intra-annual variability in juvenile red drum abundance during the newly settled (October-December) and early juvenile (January-March) life stages for Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. Catch per unit effort (CPUE) is number of individuals per seine haul (~300m²). Note different scales on each plot.

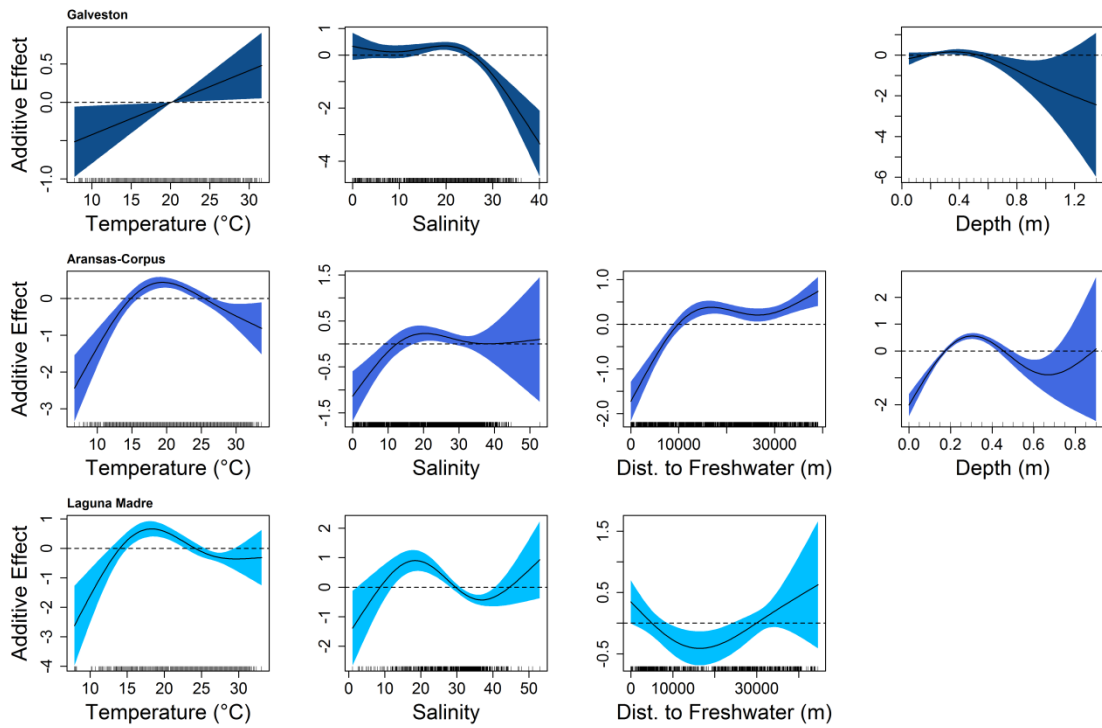


Figure 15. Response plots showing the influence of abiotic variables on the abundance of newly settled juvenile red drum in Galveston Bay (top), Aransas-Corpus Bay (middle), and Laguna Madre (bottom) from final generalized additive models (GAMs). Variables shown include temperature, salinity, distance to freshwater (dist. to freshwater), and depth. Solid lines represent smoothed values and shaded areas represent 95% confidence intervals.

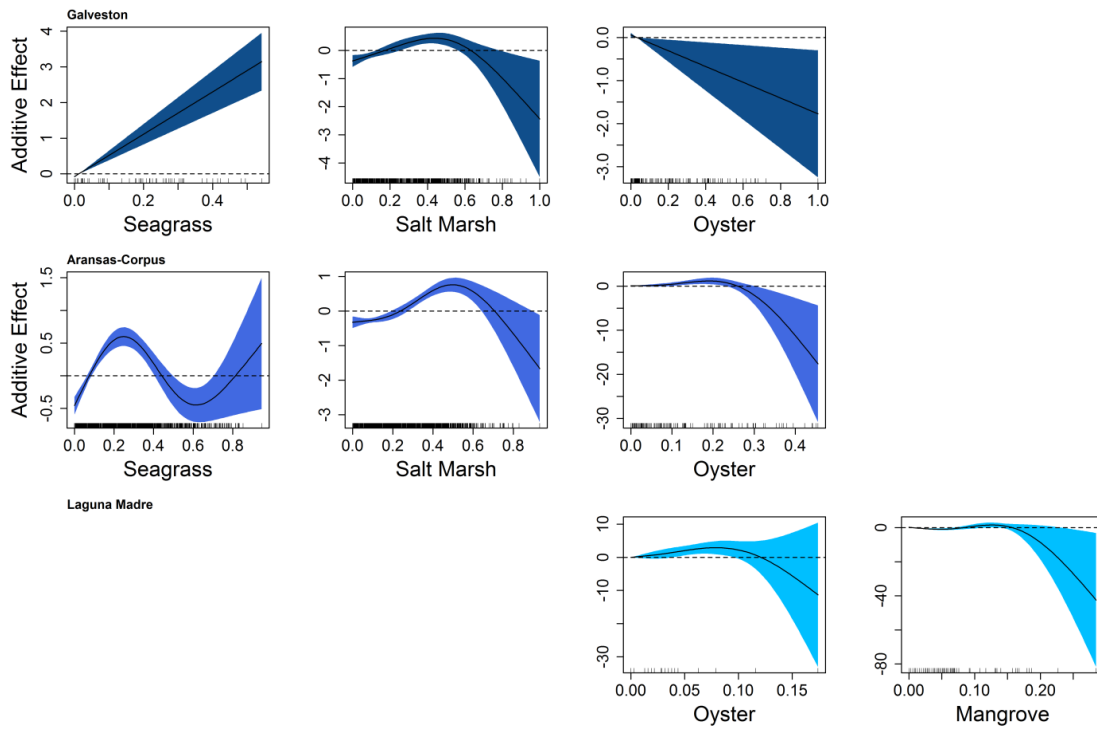


Figure 16. Response plots showing the influence of biotic variables on the abundance of newly settled juvenile red drum in Galveston Bay (top), Aransas-Corpus Bay (middle), and Laguna Madre (bottom) from final generalized additive models (GAMs). Variables shown include proportion of seagrass, salt marsh, oyster, and mangrove coverage within a 300 m radius of the sampling site. Solid lines represent smoothed values and shaded areas represent 95% confidence intervals.

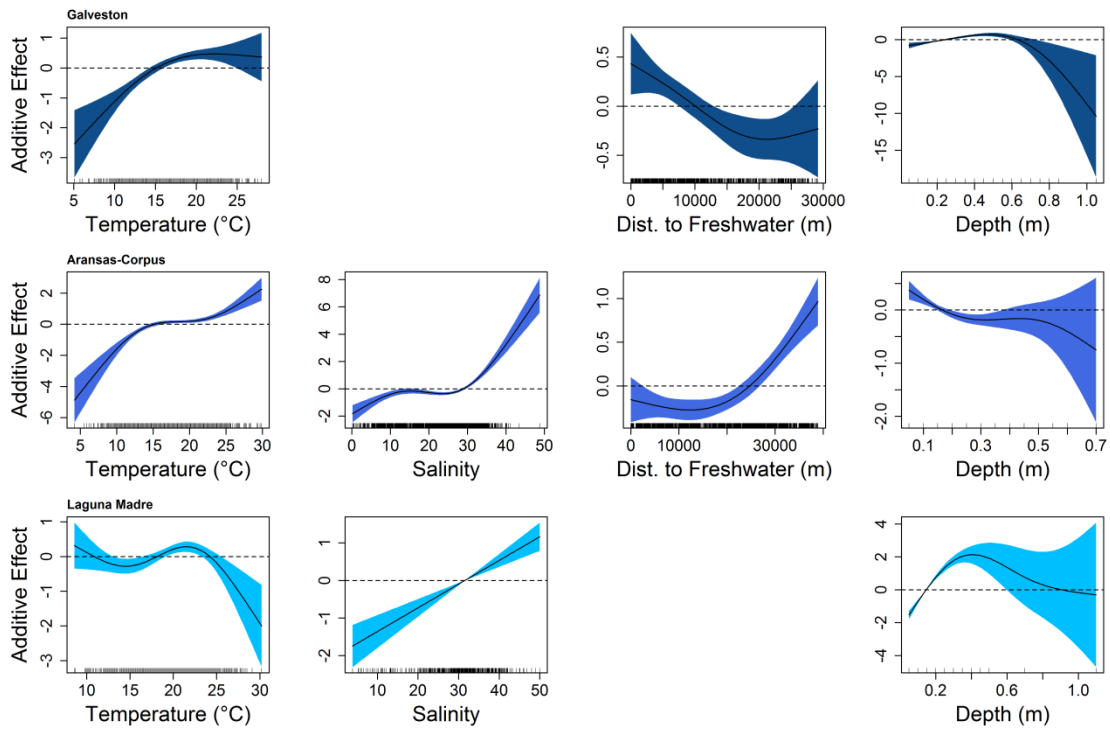


Figure 17. Response plots showing the influence of abiotic variables on the abundance of early juvenile red drum in Galveston Bay (top), Aransas-Corpus Bay (middle), and Laguna Madre (bottom) from final generalized additive models (GAMs). Variables shown include temperature, salinity, distance to freshwater sources (dist. to freshwater), and depth. Solid lines represent smoothed values and shaded areas represent 95% confidence intervals.

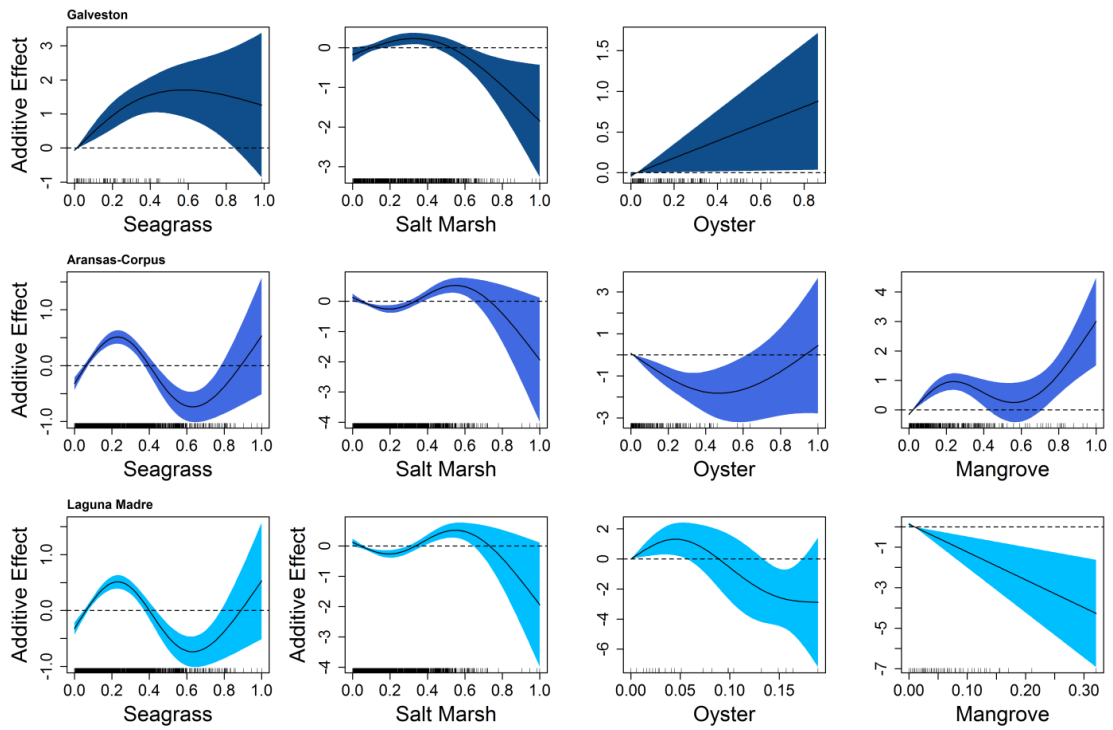


Figure 18. Response plots showing the influence of biotic variables on the abundance of early juvenile red drum in Galveston Bay (top), Aransas-Corpus Bay (middle), and Laguna Madre (bottom) from final generalized additive models (GAMs). Variables shown include proportion of seagrass, salt marsh, oyster, and mangrove coverage within a 300 m radius of the sampling site. Solid lines represent smoothed values and shaded areas represent 95% confidence intervals.