

THE MOVEMENT ECOLOGY OF LARGE, MOBILE FISHES IN NORTH CAROLINA
ESTUARIES

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ABSTRACT

Matthew Dylan Kenworthy: The Movement Ecology of Large, Mobile Fishes in North Carolina Estuaries
(Under the direction of F. Joel Fodrie)

Linkages between availability of healthy coastal habitats and sustainability of fish populations has been an important driver of marine ecosystem conservation and restoration efforts. Yet, identifying what exactly constitutes critical habitat remains challenging. Key to identifying the value and function of estuarine habitats in supporting fish production is quantifying spatiotemporal use of target habitats by fishes. However, this is complicated by the fact that fish move over multiple spatiotemporal scales. I explored the movement ecology and habitat selectivity of recreationally important fishes in multiple North Carolina estuaries addressing three major questions: 1) Does the movement behavior of a large predatory fish (red drum) enhance landscape-level connectivity among estuarine saltmarsh complexes? 2) Does a large predatory fish (red drum) express fine-scale habitat selectivity within a saltmarsh complex that can be used to infer critical habitats in estuarine seascapes? And 3) Does the size, nature of emergent structure, and landscape context of man-made oyster reefs influence utilization by red drum, black drum, and southern flounder in the New River Estuary (NRE)? Additionally I examined the advantages and disadvantages associated with sampling spatial ecology of fish using traditional gears vs advanced acoustic telemetry. Dispersal, activity space, and residency by red drum identified limited movement between marsh complexes, suggesting minimal linkages among spatially separated habitat complexes occur on a sub-annual scale. Fine-scale

analysis of red drum habitat utilization identified greater than expected selection for structured habitats along saltmarsh edges. In the NRE, man-made cultch reefs were visited by our focal species in similar modes and frequencies as unstructured habitats following the destructive harvest of oysters. We observed a greater volume of detections for black drum at the larger, more structurally complex artificial reefs although no distinguishable relationships were observed for red drum and southern flounder. Finally, because traditional gears sample a greater quantity and variety of individuals and species, they have been utilized primarily in studies evaluating community based research questions while telemetry has been linked with research requiring greater spatiotemporal resolution of fish behavior. This research both expands on and corroborates previous studies analyzing the movement ecology of fishes. These data will better inform stakeholders about the value of various estuarine habitats and guide managers in prioritizing conservation and restoration plans to maximize ecosystem function and production.

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LIST OF SYMBOLS AND ACRONYMS

%	percent
<	less than
>	greater than
±	plus or minus
σ	standard deviation
Δ	delta (difference in)
μ	average
ANOVA	Analysis of Variance
C	Celsius
Cm	centimeter
m	meter
mm	millimeter
km	kilometer
n	sample size
RTK GPS	real time kinematic global positioning system
SE	standard error
t	time
ppt	parts per thousand
VR2W	Name of VEMCO single channel receiver
VUE	VEMCO software used for communicating with VR2W receiver
LOTEK	LOTEK Wireless Fish & Wildlife monitoring system

CHAPTER1: MOVEMENT ECOLOGY OF A MOBILE PREDATORY FISH REVEALS LIMITED HABITAT LINKAGES WITHIN A TEMPERATE ESTUARINE SEASCAPE¹

Introduction

Marine ecosystems are typically comprised of heterogeneous mosaics of distinct habitat patches (i.e., seascapes). Identifying the value and function of habitats within the seascape is a central component of efforts to conserve and protect estuarine habitats (Bostrom et al. 2011). As ecologists and managers incorporate ecosystem-level approaches into research and decision making in marine environments, they have drawn on studies quantifying the degree of connectivity that results from the exchange of nutrients, pollutants, pathogens, sediments, and organisms (i.e., fish, birds, and mobile invertebrates) across habitat boundaries within seascapes (Polis et al. 1997). Fish movement, often considered one of the most influential factors in mediating habitat connectivity (Sheaves 2009), within and among these habitat mosaics can affect species interactions (Baggio et al. 2011), foraging behaviors (Beets et al. 2003), ecosystem resiliency, biodiversity (Olds et al. 2012), reproduction (Bolden 2000), recruitment success (Berkstrom et al. 2012), and nutrient transfer (Meyer et al. 1983). Therefore, enhancing our understanding of fish movement patterns within and between various estuarine habitats is critical

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to the management and conservation of fish populations and habitats on which they depend (e.g. identifying discrete stock units).

Mobile fish species capable of traveling large distances (i.e. >5 km/day) increase the linkages and potential for connectivity among habitats within estuarine seascapes (Rosenblatt and Heithause 2011; McCauley et al. 2012; McMahon et al. 2012). Fish behavior can be highly variable, with a number of factors affecting a fish's decision to move. For example, movement and habitat choice can vary with individual preference and habitat complexity (Poppo and Hunte 2005), different degrees of predation pressure (Martin et al. 2010), resource availability (Hammerschlag et al. 2010), seasonally (Barbour et al. 2014; Ketchum et al. 2014), and between contingents of fish (Afonso et al. 2009). Here, we explore the movement behaviors of a relatively large mobile predator between different marsh complexes within a temperate estuary and the potential implications of this behavior on seascape-level connectivity of marsh complexes.

Salt marsh (*Spartina alterniflora*) complexes are often the dominant shoreline habitat within temperate estuarine ecosystems, and are typically comprised of a mosaic of salt marsh, seagrass, oyster reef, and mud/sand flat that are separated by deeper channels or extended sand/mud flats from other structured habitats (most typically, other marsh complexes). Connectivity, resulting from fish movement, has been explored at small (10's of m) spatial scales in relation to movement of considerably less mobile fish (Able et al. 2012). Estuarine scale (kms) connectivity among marsh complexes, however, is less well characterized. Identifying the level of linkages between individual saltmarsh complexes would help frame our understanding of whether whole estuaries function as the fundamental unit of "habitat" for large mobile fishes, versus a series of relatively discrete habitat units for subpopulations of a given species.

Red drum (*Sciaenops ocellatus*), common in estuaries from Virginia to Texas, is highly sought after by recreational fishermen. As sub-adults (up to age five), red drum inhabit estuarine marsh complexes and near-shore habitats and forage on small fishes and crustaceans (Scharf and Schlacht 2000). Individuals are capable of traveling large distances (> 10 km/week) and are often found occupying a variety of estuarine habitats across a wide range of salinities in temperate estuaries (Bacheler et al. 2009a; Bacheler et al. 2009b). Because they are considered highly mobile and use a wide range of estuarine habitats, red drum are presumed to increase the connectivity of spatially separated saltmarsh complexes within estuaries over tidal, diel, and seasonal scales.

Understanding movement behavior of fish is challenging due to limitations in observing individuals directly. Yet, the use of acoustic tracking methods is increasing and overcoming long-standing impediments to monitoring fish movements. In particular, acoustic tracking promotes monitoring of movement and behavior of individual fishes across broader spatial and temporal gradients. The objective of this study was to quantify red drum movement patterns, more specifically temporal variation in dispersal and activity space (home range), with the overarching goal of assessing how fish behavior influences linkages between salt marsh complexes. We asked three primary questions regarding the movement behaviors within this estuarine seascape: 1) At what rate did individuals disperse throughout the estuary and into new areas? (2) What was the activity space of individual red drum, and did it vary throughout the study? And (3) Did individuals express high levels of residency within individual marsh complexes in the study array or frequently move among them?

Methods

Study Area

We acoustically tracked the movement of 34 sub-adult red drum over five months within a temperate estuary near Cape Lookout, NC (Fig. 1.1). The shallow estuary of North River and Back Sound covers an area of 68 km² from Beaufort Inlet (western extent of study system) to Bardens Inlet at Cape Lookout (eastern extent). The estuary contains multiple saltmarsh complexes, large expanses of shallow un-vegetated bottom, and deeper channels. Within the study area, we deployed an array of 25 Vemco VR2W hydrophones to detect red drum movement, specifically among four distinct salt marsh complexes (Fig. 1.1).

Within each marsh complex, multiple hydrophones were deployed to increase the probability of detection when fish were present. For our analysis, hydrophones were grouped according to their associations with individual marsh complexes or classified as “non-marsh” (Fig. 1.1). Non-marsh stations were located in deeper channels and mud/sand flats, which were presumed to be travel corridors. The hydrophone stations were grouped as follows: Carrot Island Marsh (CIM) stations: 1, 4, 5, 9; Middle Marsh (MM) stations: 10, 13, 14, 15, 19; North River Marsh (NRM) stations: 8, 11, 12; Back Sound Marsh (BSM) stations: 21, 22, 25; and non-marsh complex stations: 2, 3, 6, 7, 16, 17, 18, 20, 23, 24 (Fig. 1.1). The VR2W omni-directional hydrophones had a detection range of approximately 350 m in this study system based on range detection tests conducted at the start of the study.

Tagging and Tracking

We collected sub-adult red drum (550 ± 15 mm total length, mean $\pm$ 1 standard error [SE]) from different locations within the study area via hook and line ($n = 24$) or large mesh (12.7 cm mesh) gill nets ($n = 10$) during July-October 2011 (Table 1.1). A coded acoustic

transmitter (LOTEK Wireless Inc. MM-MR-11-28, also used in a companion fine-scale tracking study, see Fodrie et al. 2015) was implanted into the body cavity of each fish following procedures similar to Dresser and Kneib (2007). These transmitters emitted both LOTEK Wireless and Vemco coded signals, and therefore were all detectable with the VR2W (Vemco) receivers. Following tag implantation, fish were held for 24 hours for observation before being released into the southwestern-most bay within the MM complex (Fig. 1.1). Fish monitored in this study were the same individuals tracked in a companion project analyzing fine-scale habitat use within MM, therefore requiring all fish to be released in the same location (Fodrie et al. 2015). Individual fish were released intermittently starting July 12th, with the last fish being released on October 9th. At regular one-minute intervals, the transmitter emitted a pulsed chirp unique to each fish, which was used to identify the presence of each individual within range of a hydrophone. For each detection, the hydrophone recorded the transmitter ID, date, and time information, and we downloaded these data monthly. Due to potential discrepancies in behavior as a result of capture, tagging, and subsequent release back into the environment, we excluded detections during the first 24 hours after being released from our movement analyses. Additionally, as a result of using a single-release location, extrapolating patterns and processes to fish being released in other marsh and non-marsh complexes could be limited; however, the faunal communities and the quality and quantity of available habitats in MM are representative of the marsh complexes in this estuary (sensu Baillie et al. 2015). Therefore, we hypothesize that red drum would behave similarly if released in other, similar marsh complexes. Prior to analysis, we used the false detections analyzer within VEMCO's data processing software (VUE) to remove any false detections. Additionally, we examined the detection data to ensure that all detections were from live individuals. A deceased individual can be identified when a transmitter

is detected continuously at a single hydrophone, with no detections occurring at any other stations, for extended periods of time.

Dispersal Patterns Away from Middle Marsh Release Location

Understanding connectivity in estuarine systems requires knowledge of the rate at which fish move throughout the estuary over hours to months. We calculated the rate of dispersal away from the release location in the southwestern-most embayment within MM. Red drum detections were separated into 10, six-day time bins, roughly representing weeks since being released into the estuary (weeks at liberty thereafter). We then established three detection metrics: 1) the raw number of detections (total detections thereafter), reflecting the number of times all individuals were detected, collectively, at each hydrophone during each week at liberty; 2) the number of individuals that visited each hydrophone during each week at liberty; and 3) a weighted number of detections, defined as “relative occurrence”, at each hydrophone during each week at liberty. We chose to look at the number of fish visiting hydrophones to supplement the detection volume data (i.e. total detections). Instead of using just the number of total detections, which for any individual hydrophone or group of hydrophones could result from ‘residency’ of a single fish, we also wanted to evaluate how many individuals were detected at each hydrophone during each week at liberty. The third metric was designed to address a potential bias of individuals with disproportionately higher number of detections “swamping” total detection (metric 1) patterns. To accomplish this, we standardized total detections by dividing a fish’s number of detections at each hydrophone by the total number of detections collectively for that individual at all hydrophones. In doing so, “relative occurrence” at individual hydrophones was scaled between 0 and 1 for each week at liberty for each fish. Each fish’s relative occurrence value at each hydrophone was then summed to generate final relative occurrence values for analysis.

We adopted the general approaches of inspecting animal movement outlined by Ergon and Gardner (2014) by quantifying dispersal patterns as changes in the three detection metrics across our hydrophones, each of known distance from the release point in MM, through time. We first plotted the relationship between our detection metrics at each hydrophone and the straight-line distance from the release location to the respective hydrophone for each weekly time bin (Fig. 1.2A). Next, normal distribution curves were fit through the data points to characterize the distribution of the detection metrics for each weekly bin. We used the resulting standard deviation (sigma [σ]) from the weekly normal distribution curves to represent the relative range of fish distribution (measured in kilometers). For the analysis, we used two standard deviations (2σ) representing 95% of the distribution range. This value therefore represented the distance from the release location in which 95% of fish detections occurred during that week, hereafter referred to as “relative distribution”. As fish dispersed from the release location, the distribution of detections as a function of distance (of hydrophones) from the release location should “flatten”, resulting in increasing 2σ values over time (Fig. 1.2B). By week 7 in our study the distribution of detections calculated from total detection and relative occurrence metrics had flattened to the point that 2σ values were unreliably large, and therefore we ceased to evaluate relative distribution beyond this point. When analyzing the number of individuals detected at each hydrophone (detection metric 2 listed above), 2σ became unreliably large after week 5. Dispersal rate, the change in 2σ over time ($\Delta 2\sigma / \Delta t$) (t = time), were calculated from the logarithmic trend lines fit to weekly relative distribution values. Dispersal rates were calculated through seven weeks at liberty for each detection metric.

Activity Space

In addition to quantifying the mean dispersal rate of tagged red drum over the duration of the study, we quantified weekly activity space size through time to examine if fish revisit the same areas or continuously explore new areas. First, we calculated the center of activity (COA) for each fish using the latitude and longitude coordinates of each hydrophone as suggested in Simpfendorfer et al. (2002). We weighted these values by the number of detections at each hydrophone visited during each week at liberty. Standard deviation (σ) values resulting from calculating the mean latitude and longitude components of the COA were averaged to obtain a single value representing the radius (m) of primary activity space for each week at liberty. Similar to dispersal calculations, we used two standard deviations (2σ) for the radius (m) of weekly activity space, which reflected 95% of all detections (per each individual fish within each week) occurring within these boundaries.

Next, we explored temporal variation in the weekly activity space of fish by calculating cumulative activity spaces. Cumulative activity space was calculated in the same manner as for weekly measurements; however, the cumulative measurement included detections from that week and all previous weeks since release. If fish were occupying completely new areas from week to week, we expected to see cumulative activity space continue to grow linearly through time (Fig. 1.3A). Alternatively, if a fish revisited areas over time, suggestive of higher site fidelity, we expected the cumulative activity would grow initially, then asymptote over time (Fig. 1.3A).

Residency

To examine patterns of residency and exchange of fish among individual marsh complexes, we calculated the probability of fish moving between each of the marsh complexes in

our study area. Each day that an individual red drum was detected, we randomly selected one detection that day and recorded the location of that detection (primary detection). Relative to the time stamp of the primary detection, we identified the location of that same fish twenty-four hours later, or as soon as possible thereafter, based on the marsh complex groupings above (subsequent detection). We chose a twenty-four-hour time step to allow for two full tidal cycles and one day-night cycle, both of which can impact fish movement behavior and habitat choice (Popple and Hunte 2005; Dresser and Kneib 2007). This procedure was repeated each calendar day for which each individual was detected throughout the study. We conducted 100 iterations, with replacement, of this sampling procedure to ensure that a representative selection of randomly selected detection data points were incorporated. Therefore, for each day a fish was detected, we performed this procedure using 100 randomly selected detections. From these observations, we created a connectivity matrix identifying the probabilities that individuals observed in a given marsh complex (primary detection) will be relocated in the same marsh complex, a different marsh complex, or a non-marsh location after 24 hours (subsequent detection). Probabilities ranged from 0, low chance of being detected in subsequent location, to 100, high chance of being detected in subsequent location. A high probability of being detected within the same marsh complex suggests high residency. Further, we explored the consistency of these behaviors over time by conducting the same analysis with time lags of 48 hours and one week following the primary detections.

Finally, we assured that the uneven distribution of hydrophones within the marsh complexes (e.g. MM contained five hydrophones while the others had 3-4 each) did not significantly alter our observations and understanding of movement behavior. We accomplished this conducting our residency analysis with two hydrophones removed from MM. We selected

the three hydrophones with the most detections and ran our analysis again three times with all combinations of two of these three hydrophones being removed from the dataset. Therefore, for each subsequent run of the analysis, MM was represented using only three hydrophones. Due to consistencies in our original test for residency patterns using different time lags as well as the consistency in the re-analysis of the dataset with a 24-hr lag, we did not perform this test using time lags of 48-hr or 1-week. The resulting detection probabilities did not differ notably from the original analysis therefore we proceeded to include all hydrophones from MM in our subsequent analysis of residency patterns.

Fishermen Recaptures

Throughout the study, recreational and commercial fishermen reported occurrences of capturing our tagged red drum. Using the date and location of the reported captures, we calculated the number of days at liberty between release to recapture and the straight-line distance from the release location to the recapture location. We examined the correlation between days at liberty and distance from the release location to suggest whether individuals exhibited random (low correlation) or non-random (high correlation) movement away from the study area. Correlation analysis was conducted in JMP Pro12.

Results

We recorded 51,987 detections overall, averaging $1,625 \pm 593$ (mean $\pm$ 1 standard error) detections per fish from 32 of the 34 tagged individuals (Table 1.1). The two individuals that were not detected were recaptured outside of the study array by fishermen indicating that these individuals simply left the array without being detected. Only four of those 32 fish were detected less than 100 times. On average, individuals visited 5 ± 1 hydrophone stations and the number of days that individuals were recorded within the hydrophone array ranged between 0 and 126 with

an average of 33 ± 5 days at liberty. Six individuals were detected visiting a combination of three marsh complexes while another 13 were only detected in two complexes. The remaining 13 fish were detected only in the MM complex. Of the 34 fish released, nine individuals were recaptured by fishermen during or following our 5-month tracking effort. The time at liberty of these nine fish ranged from 2 days to 425 days and the straight line distance from the release location to the recapture location varied from 0 km up to 38 km. There was no distinguishable relationship between days at liberty and distance from release location to recapture location (Pearson's $r = <0.01$).

Dispersal

Over the course of the study, all three dispersal metrics indicated initial dispersal from the release location during the first two weeks followed by minimal dispersal within the study area over the remainder of the study (Fig. 1.2C). Relative distribution calculated from total detections indicated that fish dispersed to a range of 1.69 km during the first week and 3.44 km after two weeks. The change in relative distribution each week from week three through week seven was less than 0.50 km. Initial dispersal rate calculated based on total detections was 2.09 km/week during week one before falling below 0.75 km/week during the remaining six weeks (Fig. 1.2D). Distribution range observed from measurements of relative occurrence was similar to that measured by total detections during the first (1.33 km) and second (3.30 km) weeks at liberty followed by minor fluctuations through week seven (Fig. 1.2C). Based on the relative occurrence of fish, the calculated dispersal rate increased slightly from week one (1.13 km/week) to week two (1.34 km/week) followed by a continuous decline through week seven (Fig. 1.2D). Finally, the distribution range observed from measurements of the number of fish at each hydrophone displayed the greatest increase during the first week (2.77 km) followed by

fluctuating distribution range through week five (Fig. 1.2C). Dispersal rate calculated based on number of fish at each hydrophone was high during week one (2.78 km/week), followed by a large reduction in dispersal rate between week two (0.63 km/week) and week five (0.20 km/week) (Fig. 1.2C-D).

The average of all three detection metrics indicated that after the first two weeks at liberty, the range of dispersal was approximately 3.29 km, which was comparable to the distance across the MM complex from the release location (2.73 km). Although dispersal measurements were calculated to represent distribution in all directions, the minimal number of detections at hydrophones one through six to the west of MM (0.08% of total) indicated that the dispersal direction was predominantly towards the east and north of the release location, along the main axis of MM.

Activity Space

Weekly mean radius of activity space ranged from 286 m to 1007 m, with an overall average of 686 ± 16.1 m (mean radius $\pm$ SE), and did not change appreciably over time (Fig. 1.3B). Calculations of cumulative activity space indicated that the greatest increase in mean radius occurred during week one (756 m) and week two (925 m) (Fig. 1.3C). The size of the cumulative activity space increased by small increments (<10% per week) over the remaining eight weeks of observations. Overall, the fish displayed only a 20% increase in the radius of their cumulative activity space between week two and week ten. Similar to results from dispersal patterns, the cumulative activity space after two weeks at liberty (2.69 km²) scaled approximately to the area of the MM complex (2.75 km²).

Residency

The connectivity matrix indicates the probabilities of fish remaining in the same location as the primary detection (highlighted values along the diagonal of the matrix; Table 1.2) or moving to a new location (non-highlighted values; Table 1.2). Movement probabilities indicated that a fish had a >85% probability of being detected in the same marsh complex after 24 hours in three of the four marsh complexes (BSM: 86.04%; MM: 93.34%; NRM: 98.87%). Fish within CIM were the least likely to remain in the same complex (connectivity index = 50%). Fish initially detected at any of the non-marsh locations had a greater likelihood of being detected at MM (48.5%) compared to being detected again at a non-marsh complex location (40.15%).

In general, when fish were not detected in the same marsh complex after 24 hours from the primary detection, they were most likely to be detected in the MM complex during subsequent detections. There was evidence for a lack of direct linkages (i.e. subsequent detection probabilities equal to zero) between several marsh complexes (MM-NRI, BSM-CIM, and NRM-BSM). Finally, none of the fish in this study were detected at either of the two stations located in the northern part of North River (stations 6 and 16), suggesting that tagged fish did not move to marsh complexes in the upper River. Extending the time lag between primary and subsequent detections resulted in very similar patterns of residency within BSM, MM, and NRM. The likelihood of being detected in the same marsh complex 48 hours and 1 week later remained >86% in all three marsh complexes. Conversely, fish originally observed in CIM had zero probability of again being detected in that marsh complex after 1 week. When primary detections were observed in CIM, these individuals were now most likely to be detected in NRM after one week.

Discussion

Patterns of red drum dispersal, activity space, and residency suggested limited movement between similar saltmarsh complexes by a mobile fish during our five-month study. Dispersal and cumulative activity space metrics indicated that there was minimal sustained occupation of areas outside of the MM complex prior to emigration from the entire study array (further supported by fishermen recapture data). Residency analysis also corroborated dispersal and activity-space data; further suggesting limited movement between the marsh complexes we monitored. Thus, our results imply that red drum induce minimal linkages among these spatially separated habitat complexes on a sub-annual scale.

Limited seascape connectivity in this study highlights the potential for these saltmarsh complexes to represent relatively isolated, discrete food webs within the estuary (Sheaves 2009). This runs counter to suggestions that mobile consumers facilitate nutrient exchange within estuaries through consumption and excretion, and may impact primary productivity in adjacent habitats when consumer movement between habitats is high (Allgeier et al. 2013; Hyndes et al. 2014). Rather our results suggest that consumer-driven transfer of nutrients may be primarily a local phenomenon, with relatively tighter recycling within each marsh complex. Additionally, red drum could potentially impose greater predation pressure locally on their prey if movement away from their preferred marsh complex is limited. Conversely, seasonally high abundances of food resources throughout the lower estuary could provide fitness incentives to limit movement away from MM, or any marsh complex in the lower North River (Dudley and Judy 1973; Williams 1955).

Assigning value to individual habitats and seascapes is an essential component to the management of fish populations and the habitats they use. Preferred habitats, measured by the

amount of time fish rely on those habitats and the benefits they provided to the success of the population, weigh heavily when evaluating habitat value (sensu Nagelkerken et al. 2015). Although red drum demonstrated high levels of residency within MM in this study, comparing this marsh complex as a preferred location to the alternative complexes is beyond the scope of this study given a potential bias in releasing all fish within this marsh complex. Nonetheless, we expect that red drum would behave in a similar manner if released in other marsh complexes due to similarities in fauna and habitat (Baillie et al. 2015). The few individuals (three) that moved into one of the alternative marsh complexes for extended periods during the study, with the exception of fish moving to CIM, displayed high residency for their new location. Although two of these fish returned to their initial capture location in NRM, there is little evidence suggesting that red drum movement is influenced by any homing behavior such as that previously documented for some large bodied fish (Taylor et al. 2017). Fourteen of the sixteen individuals initially captured in NRM remained in the MM system during the study and only two out of thirty translocated fish were observed returning to their initial capture location. Reflecting the results observed in this study, other fish in the population would be suggested to maintain high levels of residency within the marsh complex they occupy.

Ontogenetic migrations of red drum generally shift the distribution of 1-3 year-old fish to lower, more saline portions of coastal estuaries (Bacheler et al. 2009b). However, this pattern is not all inclusive as two-year-old fish, equivalent to those used in our study, are still known to occupy low salinity (< 10 ppt) waters of North Carolina estuaries (Bacheler et al. 2009a) specifically the upper North River estuary (M. Kenworthy, personal observations). Regardless of expectations that red drum in our study system would move to occupy this region of the estuary, none of the tagged red drum were detected at our two upper estuary stations. Furthermore, only a

limited number of fish (four) were detected as far up-estuary as NRM (Fig 1.1). Our data contribute to the growing consensus in the literature that suggests red drum rarely move upstream as sub-adults (Dresser and Kneib 2007; Bacheler 2009b). Occupation of the upper estuary by similar age class fish is likely a result of individuals either settling in this region and remaining or individuals arriving during spring months when a large portion of the sub-adult population re-enter and distribute within the estuaries (Bacheler et al. 2009b). Connectivity among upper estuary and lower estuary seascapes therefore is likely influenced more by ontogenetic migrations or suggested re-entry of the red drum population into the estuary. The mechanism driving this subpopulation structure deserves further research attention.

Overall, red drum displayed high levels of residency within the MM complex with limited seascape linkages. However, some fish were observed making intermittent excursions between MM and both CIM and BSM, potentially establishing linkages with these other complexes. These excursions almost always occurred during nighttime hours and were short in duration. These movement patterns could reflect foraging excursions to the habitats located between the associated marsh complexes. For example, the sandflats between MM and BSM contain isolated patches of seagrass, which red drum could be targeting during preferred crepuscular and nighttime foraging hours (Facendola and Scharf 2012). In comparison, the sandflats between MM and CIM do not contain seagrass patches. This area, located near one of two main channels flowing out of North River, is a potential corridor for crustaceans (crabs and shrimp) emigrating out of the upper North River estuary at night, and could be serving as a source of food. Therefore, these excursions could facilitate linkages within the estuarine seascape via nutrient exchange between unstructured habitats surrounding MM and the MM complex, similar to that observed in other ecosystems (e.g. coral reefs) (Beets et al. 2003), even if red

drum are not consistently connecting distinct marsh complexes within this estuary. Following the flow of energy within coastal ecosystems is important for understanding the values and contributions of individual towards productivity within an estuary (Heck et al. 2008). Although these assumptions are speculative without direct measurements of nutrient exchange within the system, identifying the movement behaviors of fish with the capacity to facilitate this nutrient exchange is critical to identifying potential energy transport dynamics within this estuary.

The spatial and temporal scale at which ecological processes are observed can influence our understanding of dynamics within an ecosystem (Levine 1992). For instance, over the time frame of this study, the distance between marsh complexes could play a crucial role in assessing linkages among them (i.e., marshes in our study were relatively far apart and therefore connectivity was low). However, considering previously reported daily movements for red drum (3.4 ± 0.6 km; Dance and Rooker 2015), we do not anticipate that this drove our results. On average, the straight-line distance between marsh complexes in our array was less than two kilometers, except for the distances between BSM and both CIM and NRM, which were each ~ 5 km. We do acknowledge, however, that the location of MM in the middle of the study array could have contributed to the higher degree of connectivity of this marsh complex relative to the other complexes we monitored.

Identifying variations in spatial and temporal movement patterns of animals can refine our understanding about life history patterns of fish and the value of the habitats they utilize (Secor et al. 2001; Drymon et al 2014; McMahon et al. 2012). Specifically, regional (upper vs lower estuary) and habitat-specific (marsh complexes) isolation of fish groups could have implications for population sampling regimes, identification of essential fish habitats for sub-adult red drum, and management of commercial and recreational fishing efforts. Our results

support previous studies suggesting that individual red drum express high residency in specific locations (Dresser and Kneib 2007; Bacheler et al. 2009b; Reyier et al. 2011; Dance and Rooker 2015). Even fish that moved out of the study array did not appear to disperse with any apparent regularity. The lack of any defined relationship between time at liberty and distance from where they were released suggests that over the course of that time frame, those individuals likely established temporary residency in other locations along the route to the where they were recaptured. Future research could build off this study to further explore the dynamics of estuarine scale seascape linkages (e.g. between lower and upper estuary) as well as marsh complex specific residency patterns.

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TABLES

Table 1.1 Summary of 34 red drum tagged with acoustic transmitters and tracked within the array of VEMCO hydrophones within the Back Sound Estuary in central North Carolina. Fish ID's marked with an asterisk are fish that were recaptured by fishermen. Capture location indicates where fish were originally caught for this study: Jarret Bay (JB), North River Marsh (NRM), Middle Marsh (MM), Carrot Island Marsh (CIM), and Northern North River (NNR).

Fish ID	Capture Location	Release Date	Total Length (mm)	Weight (kg)	Total Detections	Stations Visited	Marsh Complexes Visited	Days at Liberty (acoustics)	Days at Liberty (recapture)	Distance to recapture (km)
RD01	JB	7/13/2011	488	1.1	249	10	3	4	-	-
RD02	JB	7/14/2011	490	1.3	9	1	1	3	-	-
RD03*	JB	7/14/2011	490	1.4	0	0	0	0	420	5.13
RD04	JB	7/14/2011	480	1.1	977	2	1	23	-	-
RD05	JB	7/15/2011	514	1.6	396	4	2	15	-	-
RD06	JB	7/15/2011	515	1.5	15	1	1	3	-	-
RD07	JB	7/15/2011	503	1.3	126	5	1	126	-	-
RD08	NRM	8/16/2011	559	2	550	11	3	76	-	-
RD09	NRM	8/16/2011	520	1.6	499	1	1	37	-	-
RD10	NRM	8/16/2011	365	0.6	101	1	1	35	-	-
RD11	NRM	8/16/2011	505	1	151	4	1	28	-	-
RD12*	NRM	8/16/2011	340	0.6	0	0	0	0	425	14.25
RD13	JB	9/3/2011	565	2	14140	6	2	62	-	-
RD14	NRM	9/3/2011	341	0.6	138	4	2	30	-	-
RD15	NRM	9/13/2011	775	4	2159	9	2	46	-	-
RD16	NRM	9/13/2011	755	4.5	38	3	1	1	-	-
RD17*	NRM	9/13/2011	549	1.6	2610	8	3	34	2	0
RD18*	NRM	9/30/2011	563	1.6	1199	5	1	32	39	38
RD19	MM	9/30/2011	556	1.5	896	2	1	43	-	-
RD20*	CIM	9/30/2011	568	2	736	7	2	49	54	2.88
RD21	NRM	9/30/2011	600	2.3	2316	4	1	26	-	-
RD22	MM	10/4/2011	610	2.2	636	5	2	31	-	-
RD23	NRM	10/4/2011	562	1.6	110	6	3	5	-	-
RD24*	NNR	10/4/2011	645	2.6	1361	7	2	49	50	0
RD25*	NRM	10/4/2011	612	2.3	301	9	2	7	7	5.86
RD26	NRM	10/4/2011	585	1.9	700	6	2	48	-	-
RD27	JB	10/6/2011	600	2	1128	7	2	21	-	-
RD28	JB	10/6/2011	612	2.3	6786	10	2	75	-	-
RD29	MM	10/6/2011	556	1.6	193	4	2	52	-	-
RD30*	NNR	10/6/2011	638	2.8	105	3	1	7	10	9.21
RD31	NRM	10/6/2011	555	1.5	1	1	1	1	-	-
RD32	NRM	10/10/2011	550	1.6	12721	9	3	70	-	-
RD33*	CIM	10/10/2011	602	2.2	314	2	2	25	179	1.83
RD34	MM	10/10/2011	534	1.5	325	7	3	43	-	-

Table 1.2 Connectivity matrix indicating the number (N) of randomly selected detections for each marsh complex and non-marsh sites and the location probabilities (%) of subsequent detection after A) 24 hours, B) 48 hours, and C) 1 week. Marsh complex names are: Back Sound Marsh (BSM), Carrot Island Marsh (CIM), Middle Marsh (MM), and North River Marsh (NRM).

		Subsequent Detection Location (=> 24 hours)					
		N	BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	3108	86.04	0.00	8.72	0.00	5.24
	CIM	608	0.00	50.00	26.81	10.69	12.50
	MM	53426	1.12	1.36	93.34	0.21	3.96
	NRM	2291	0.00	0.00	0.09	98.87	1.05
	Non-Marsh	2249	11.38	0.00	48.47	0.00	40.15

		Subsequent Detection Location (=> 48 hours)					
		N	BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	2857	86.66	0.00	9.45	0.00	3.89
	CIM	616	0.00	44.97	26.79	28.25	0.00
	MM	48867	1.69	1.20	90.62	0.54	5.96
	NRM	2146	0.00	1.07	0.00	98.93	0.00
	Non-Marsh	2124	11.35	0.00	51.84	0.00	36.82

		Subsequent Detection Location (=> 1 week)					
		N	BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	2457	86.57	0.00	12.70	0.00	0.73
	CIM	527	0.00	0.00	29.41	70.40	0.19
	MM	43743	1.89	1.39	88.71	0.94	7.07
	NRM	1805	0.00	0.00	0.00	100.00	0.00
	Non-Marsh	1684	14.55	0.00	67.52	0.00	17.93

FIGURES

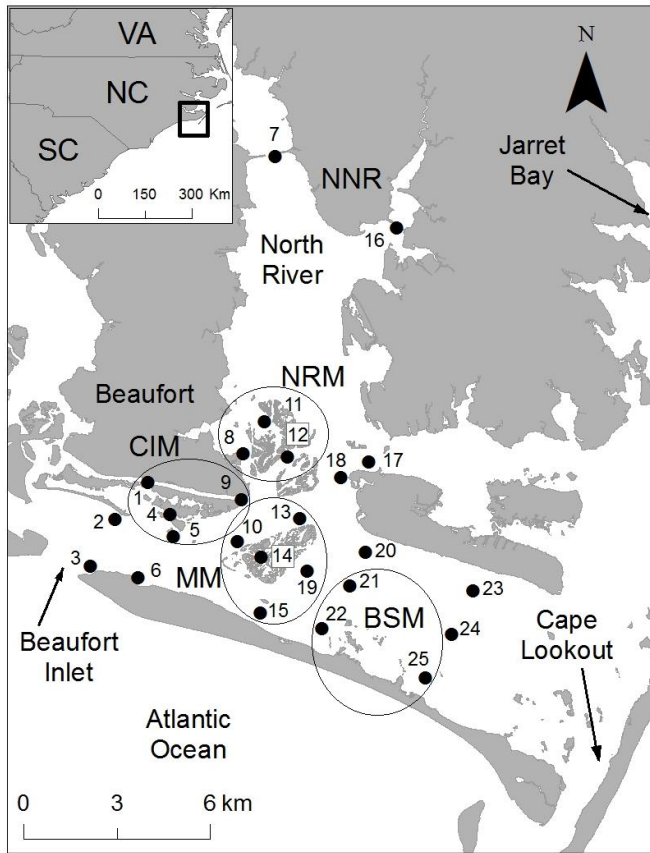


Figure 1.1 Map of the hydrophone observation network labeled with station identification numbers. Hydrophones (marked by black dots) for associated marsh complexes are contained in individual labeled circles. Locations included are Northern North River (NNR), North River Marsh (NRM), Carrot Island Marsh (CIM), Middle Marsh (MM), and Back Sound Marsh (BSM). Map was produced using ArcGis for Desktop (ArcMap 10.5). Shoreline shapefiles obtained from ESRI and the North Carolina Department of Environmental Quality (NCDEQ).

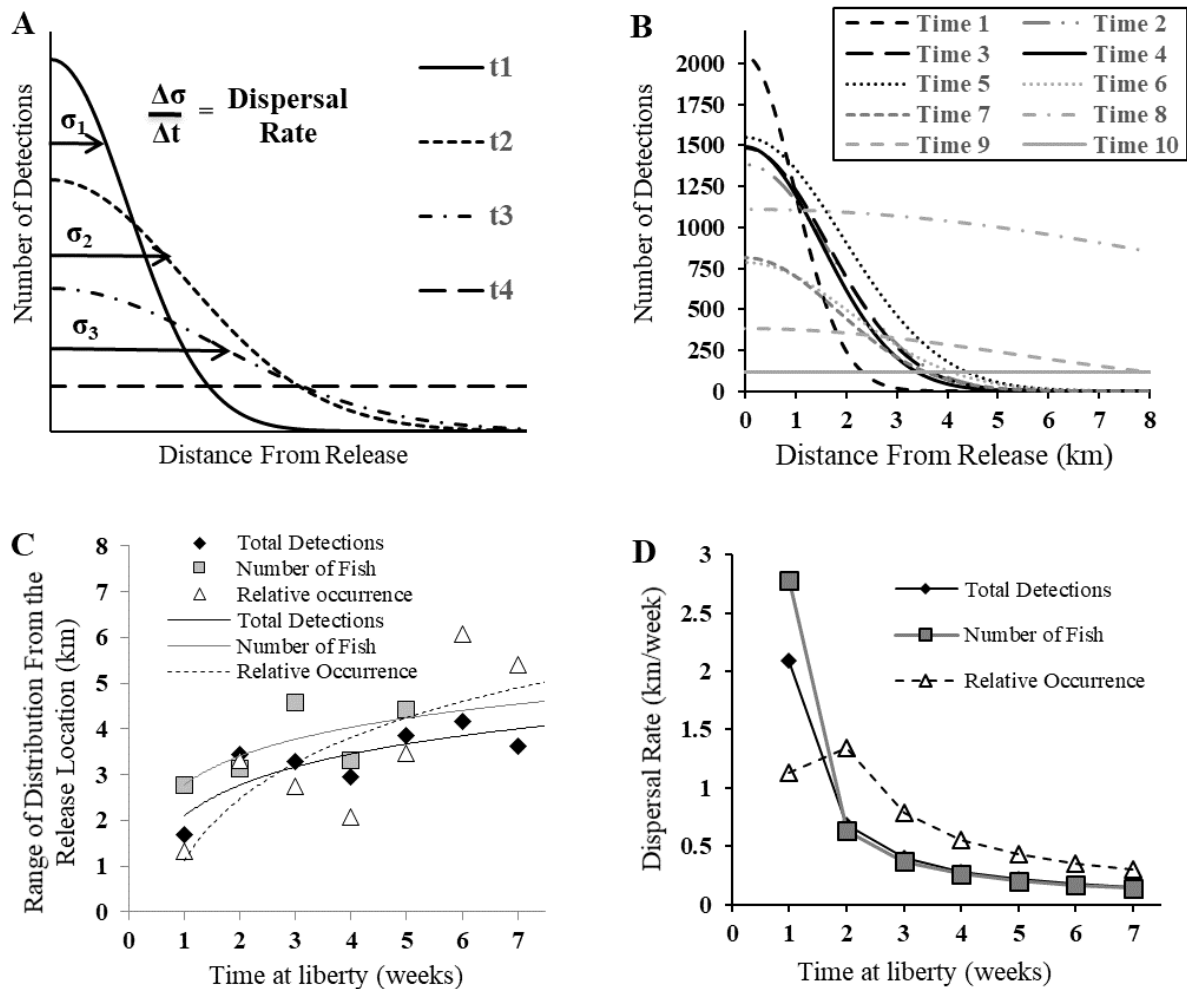


Figure 1.2 Dispersal patterns for red drum throughout the study based on distributions of the three metrics measured, (total detections, number of fish, and relative occurrence) at hydrophones of known distances from the release location. Panels represent A) theoretical expectations of weekly detection distribution change through time; B) actual total detection distribution curves for each week of the study; C) weekly range of distribution values calculated from distribution curves for each metric used; and D) dispersal rates calculated for the three detection metrics.

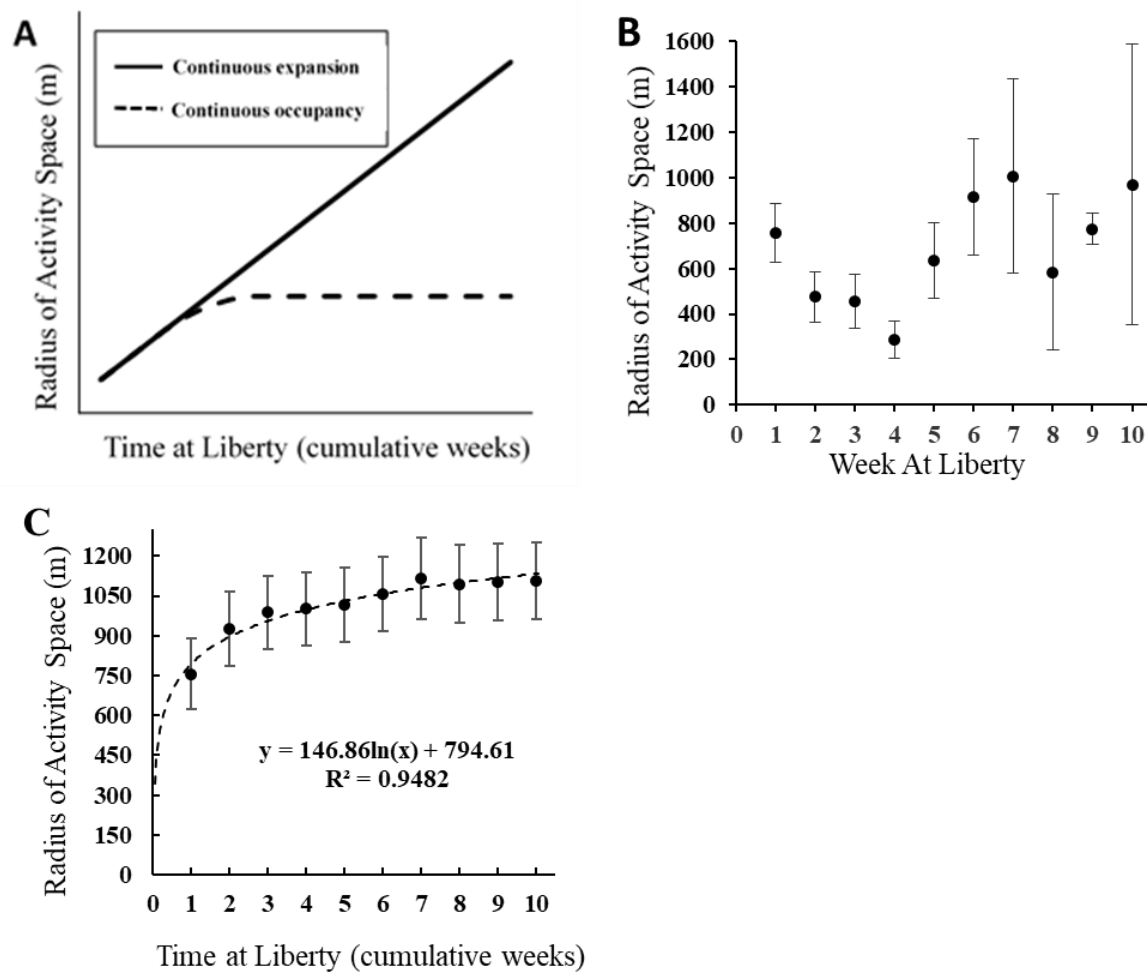


Figure 1.3 Red drum activity space measured through time. Panels represent A) two theoretical patterns of cumulative activity space growth through time indicating that fish either continue to explore new areas over time (solid line) or continue to occupy the same areas repeatedly (dashed line); B) weekly measurements of the radius of the activity space and C) measured cumulative activity space growth throughout the 10 weeks of the study.

CHAPTER 2: SPATIAL CONFIGURATION OF HABITAT WITHIN AN ESTUARINE SEASCPE MOREINFLUENTIAL THAN IDENTITY AND AVAILABILITY IN DETERMINING SELECTIVY BY A MOBILE PREDATORY FISH

Introduction

Identifying essential habitats which are most conducive to rapid growth and/or increased survival in fishes is a central component of efforts to conserve and protect estuarine habitats and ensure the sustainability of fish populations (Dahlgren et al. 2006, Bostrom et al. 2011). Key to achieving this management objective is understanding the basic habitat requirements of fish within the ecosystem. In coastal estuarine ecosystems which are composed of a variety of spatially heterogeneous but functionally connected habitats (i.e., seascapes), identifying high-quality fish habitat remains challenging (Beck et al. 2001). Estuarine dependent fishes in particular have complex habitat requirements during their life cycle which can vary along spatiotemporal gradients due to ontogenetic migration (Bacheler et al. 2009), predator avoidance behavior (Hammerschlag et al. 2010), foraging behavior (Hammerschlag-Peyer and Layman 2010), and individual specialization in behavior (Fodrie et al. 2015). Rigorous quantitative data on multi-scale habitat utilization by fishes will help stakeholders allocate limited financial and material resources towards the conservation of high value habitats to ensure sustainable fish populations.

While habitat identity is commonly recognized as a key determinant of habitat use by estuarine fishes, recent studies have highlighted the importance of context in defining ecological interactions between animals and their environment (Bradley et al. 2019). Spatial configuration of habitats has been highlighted often as a primary driver of species assemblages within estuarine seascapes. For example, at large spatial scales, species assemblages in seagrass meadows have

been demonstrated to vary with estuary geomorphology and ocean connectivity (Schrandt et al. 2018). At smaller spatial scales, spatial configuration of individual habitat patches within the seascape has been demonstrated to have significant implications on species distribution (Pittman et al. 2007, Baillie et al. 2015), predator foraging behavior (Micheli and Peterson 1999), food web dynamics (Polis et al. 1997), estuarine scale habitat connectivity (Kenworthy et al. 2018), species diversity (Yaeger et al. 2016), and function of restored habitats (Keller et al. accepted, Ziegler et al. 2018). Therefore, in order to maintain the structure and function of particular habitats, ecologists need to develop a better understanding of fish-habitat associations within the context of the larger seascape in addition to focusing on individual habitat classification.

Generating quantifiable metrics identifying the value of fish habitat is challenging (Garshelis 2000). Quantifying levels of habitat use for fish is particularly challenging in estuarine environments where a number of biotic (i.e. foraging and reproductive behaviors) and abiotic (i.e. temperature, salinity and DO) processes are acting on estuarine fish movement and assemblages (Sheaves 2016). Additionally, quality is often inferred from quantitative measures of demographic responses (i.e., catch densities) within select habitat classifications. Presumably, such measures of habitat use are reflective of relative importance to fish in terms of fitness. While, spatiotemporal catch density data has underpinned estuarine fish management strategies for decades, researchers have recently acknowledged some shortcomings (e.g., size and species selectivity, spatial limitation, infrequent sampling, etc.) associated with gear types (e.g., gill-nets, traps, videos) commonly employed to collect these data (Olin and Malinen 2003, Hubert et al. 2012). The development of high resolution telemetry provides opportunities to better analyze the spatial ecology of estuarine fishes, thereby allowing researchers to resolve discrepancies in habitat use with greater spatio-temporal resolution for a variety of species.

Evaluating habitat value using demographic data provides knowledge of species abundance and distribution, although these data alone are limited in assessing selective preference for available habitats within estuarine seascapes. Because the abundance of various resources (e.g., habitat) is not uniform in nature, a more informative evaluation of selection and preference for individual habitat patches must consider both habitat use and habitat availability (Garshelis et al. 2000). Habitat selectivity thus can be quantified according to the disproportionate selection for or avoidance of available habitats resulting from choice rather than haphazardly wandering within the environment (Johnson 1980, Manly et al. 2002). In this study we combine high resolution (sub-meter) acoustic tracking data with fine scale data of habitat distribution within an estuarine marsh complex to assess fish habitat selectivity for red drum (*Sciaenops ocellatus*). We ask two primary questions regarding habitat selectivity of red drum within this system: 1) Do red drum display selective preference for or avoidance of individual habitat classifications relative to their availability within the environment? and 2) Does spatial configuration of individual habitat patches within the seascape influence habitat selection for red drum?

Methods

Study site

We acoustically tracked the movement and habitat use of 34 subadult red drum over five months within Middle Marsh, North Carolina. Middle Marsh is a 1.5 km² marsh complex composed of a mosaic of salt marsh, seagrass, oyster reef, and interspersed mud-sand flat (Fig 2.1). We established a fine scale tracking array to monitor movement and habitat selectivity within one of the larger (100,000 m²) embayment's containing a diverse mix of natural and

restored habitats. Previous studies have indicated that large predatory fish like red drum frequently access these embayments within Middle Marsh (Grabowski et al. 2005, Kenworthy et al. 2018). Thus, we were able to explore habitat selectivity and movement behavior in a natural, open seascape composed of a variety of habitat classifications.

Using high resolution (<1m) aerial imagery, we delineated the following habitat types: 1) Sand—areas of bare, smooth substrate generally in the central portion of the study area; 2) Halo—bands of bare substrate 3–5 m in width that separated marsh and seagrass habitats. Halo bottoms were qualitatively muddier and had greater Lebensspuren densities than sand bottoms; 3) Seagrass—mixed *Zostera marina* and *Halodule wrightii* distributed as contiguous and patchy meadows across the study area; 4) Marsh—flooded *Spartina alterniflora* along the perimeter of the study area; 5) Fringing shell—loose, naturally occurring aggregates of both living and dead shell bordering marsh habitat (<25 oysters m⁻²); 6) Reef (salt marsh; SM); natural and restored oyster reefs immediately adjacent to marsh habitat (>100 oysters m⁻²). Unlike fringing shell, reefs were consolidated, raised features within the embayment; 7) Reef (seagrass; SG)—restored oyster reefs immediately adjacent to seagrass habitat and isolated from salt marsh; 8) Reef (sand flat; SF)—restored oyster reefs surrounded by a sand matrix and isolated from other structured habitats. With the exception of the reef adjacent to seagrass, all other oyster reefs in this system were intertidal.

Individual habitats within the embayment were mapped using satellite images obtained through the National Oceanic and Atmospheric Administration data bases (Geo-Eye and World View; early and middle periods) and eMap International (IKONOS; <http://www.digitalglobe.com/resources/satellite-information>). Distinct polygons for each habitat classification were generated in ArcMap 10.0 and verified using manually collected habitat

boundary positions collected using a Trimble RTK-GPS. To account for seasonality in seagrass cover (i.e., *Zostera* senescence due to heat stress), aerial images from three separate dates during the study were acquired for delineation of habitat boundaries. Thus, habitat use was evaluated during three time periods consisting of equal duration (early, July 15 up to and including August 30; middle, September 1 up to and including October 14; and late, October 15 up to and including 30 November).

Study Species

Red drum (*Sciaenops ocellatus*), common in estuaries from Virginia to Texas, is highly sought after by recreational fisherman. As sub-adults (up to age 5), individuals inhabit estuarine environments and forage on small fishes and crustaceans (Scharf and Schlicht 2000). Red drum are often considered habitat generalists because they commonly occupy a variety of estuarine habitats across a wide range of salinities in temperate estuaries including salt marshes, seagrass, and oyster reefs (Bacheler et al. 2009, Fodrie et al. 2015, Kenworthy et al. 2018). Because of the variety of habitats used by this species, a working hypothesis is that individuals for this species will utilize the habitat within our study system in proportion to its availability within the seascape.

Tagging and Tracking

We collected subadult red drum (550 ± 15 mm total length [TL], mean $\pm$ 1 standard error [SE]) from different locations within the study area via hook and line ($n = 24$) or large mesh (12.7 cm mesh) gill nets ($n = 10$) during July-October 2011 (Table 2.1). A coded acoustic transmitter (LOTEK Wireless Inc. MM-MR-11-28) was implanted into the body cavity of each fish following procedures similar to Dresser and Kneib (2007). The LOTEK tags emitted a pulsed chirp, unique to each fish, every 5 s that was used to chart each individuals' position

while in the study area. Following tag implantation, fish were held for 24 hours for observation before being released into the center of the embayment. Individual fish were released intermittently starting July 12th, with the last fish being released on October 9th. Once released, red drum were free to enter or exit the study area without further manipulation (data collection began 12 h after release to allow for acclimation). While inside of the embayment, auditory cues should have transmitted far enough to ensure that all habitats were within the ambit of individual red drum; therefore, we are confident that all individuals sampled a common resource (habitat) pool in this study.

We deployed a LOTEK MAP 600 Acoustic Telemetry system to detect acoustic signals emitted from tagged red drum and track their fine-scale habitat use. The MAP 600 uses 8 fixed hydrophones positioned to allow “line-of-sight” detection of coded signals from LOTEK transmitters. Fish positions with sub-meter accuracy were generated when signals were detected by at least three hydrophones within the array. Hydrophones were positioned within the embayment to maximize overall coverage while providing reliable detection of tagged red drum within the target habitats. Position data was superimposed on habitat maps generated for each study period to quantify the volume of detections within each habitat classifications for individual fish

Habitat Selection Indices

Habitat preference was quantified using approaches derived from studies examining diet selectivity (Johnson 1980, Lechowicz 1982, Manly et al. 2002). Habitat selection indices (HSI) identified each fish’s preference or avoidance of individual habitat classifications within the study area. Habitats chosen at random would mirror availability, whereas preference or avoidance would result in habitat use that is greater than or less than availability, respectively.

We used individual fish positions as our observational unit for habitat use analysis. This index was calculated by dividing each fish's proportion of positions within each habitat by the proportional availability of each respective habitat during individual time periods. We used log values of each quantified HSI for analysis, thus the degree of preference or avoidance for individual habitat classifications was identified by the degree of deviation in a positive (preference for) or negative (avoidance of) direction from a value of 0. Because of the potential bias of individual fish with disproportionately higher number of positions "swamping" observed trends in habitat use, we quantified the weighted mean HSI for comparisons between habitat classification and time periods. Each fishes' HSI was weighted by the individual's proportion of detections within each time period. Habitat selection indices were quantified for each habitat individually as well as all oyster reef habitats combined during each study period.

We quantified availability of each habitat classification after accounting for differences in habitat accessibility across the tidal cycle. Shallow habitats (e.g., oyster reefs) were accessible less often than deeper habitats (e.g. seagrass) thus affecting use-availability analysis. Water level data collected from a HOBO Water Level Logger (Onset Computer Corporation; ± 0.3 cm accuracy) located near the study site was integrated with bathymetry maps of the embayment to ascertain the spatial coverage (m^2) of accessible habitat at ten-minute intervals for each time period. Considering that access to a given habitat is limited by water depth, a habitat patch was only considered available when water depth was greater than 30cm because examination of position data throughout the entire study identified this as the minimum depth at which fish were detected. Bathymetry maps were generated by combining elevation data collected using a terrestrial laser scanner (intertidal habitat; see Ridge et al. 2015 for more detail) and manual transects using a Trimble RTK GPS (subtidal habitat). Availability of individual habitat

classifications for each time period was quantified as the sum of each ten-minute measurement of spatial coverage (m²).

Results

Overall, 144,320 triangulated fish positions were recorded from 27 out of the 34 tagged individuals for analysis of habitat selectivity ($5,345 \pm 1,485$ positions fish⁻¹) (Fig. 2.2). The seven individuals for which no position data was acquired were detected in a companion study (see Kenworthy et al. 2018), indicating that these individuals simply left the array within the initial 12 hours of release without returning. Only three of the 27 fish recorded fewer than 100 positions throughout the entire study. The timing of when fish were released resulted in variable numbers of fish monitored during the early (n = 8; 37,596 detections), middle (n = 20; 71,987 detections), and late (n = 10; 34,739 detections) time periods. Thirteen individuals were tracked over multiple time periods.

Throughout the study, red drum were consistently detected most in the seagrass, sand, and halo habitats. The combined quantity of positions within these habitats was greater than 80% of the total positions during each time period (Table 2.2). Apart from fringe reef habitat during the early period, the number of positions located within each of the remaining individual habitat classification never exceeded 10%. Marsh, sandflat reef, and seagrass reef (late period only) were the least used habitats (< 1% of detections during respective time periods) throughout the study. Of the four reef classifications, the proportion of positions were consistently greater within marsh (4.2% – 5.9%) and fringe reef (4.2%– 10.9%) habitats compared with sandflat (<0.1% – 0.7%) and seagrass reefs (0.1% – 1.9%). The volume of positions within all reef classifications combined never exceeded 20% of all positions during the study.

Habitat availability was substantially greater for both seagrass and sand within the array (Table 2.3). This pattern was consistent for each time period regardless of the decline in *Zostera* due to senescence. During each of the time periods, sand and seagrass habitats combined comprised approximately 93% of the available habitat. The decline of seagrass from the early (43%) to late (26%) period resulted in a subsequent increase in sand coverage from 50% to 67% during respective time periods. Halo and fringe reef comprised approximately 3% and 2% of the available habitat respectively. The remaining habitats each individually consisted of less than 1% of all available habitat within the array. Minor ($< 1\%$) fluctuations were observed in availability of the reef habitats, likely due to slight variations in water levels recorded during individual time periods.

Mean HSI over the course of the study indicated a general avoidance of sand (-0.48) and marsh (-1.48) habitats while generally preferences for the halo (0.68) and oyster reefs (0.50) (Fig. 2.3). Observed selection indices during each individual time period in these respective habitats reflected overall averages (e.g. HSI in sand was consistently negative throughout the study). Although, mean HSI for seagrass (0.04) over the entire study suggested random usage of this habitat, selection indices during the early period (-0.20) indicated modest avoidance followed by a shift to modest preference during middle (0.09) and late periods (0.25). Whereas HSI values for oyster reefs combined were consistently positive, red drum displayed variable responses in preference for individual reef classifications (Fig. 2.4). Mean HSI was consistently positive for saltmarsh reef (0.65) and fringing shell (0.31) habitats over the duration of the study. Conversely, mean HSI within sandflat reef (-1.63) reflected a consistently strong avoidance throughout the study. Selection indices for reefs located in seagrass indicated no distinguishable

preference or avoidance of the habitat classification during the early (0.01) period; however, there was a notable shift towards avoidance during the middle (-0.34) and late (-1.49) periods.

Discussion

By comparing high resolution position data with rigorous analysis of habitat availability, we were able to identify a gradient of preferences for the variety of habitats available to red drum within this saltmarsh embayment. Regardless of the greater volume of positions located within seagrass and sand, selection indices indicated that these habitats were not the most selected for by fish in this system. We observed the greatest selection for habitats proximate to, but not within, marsh habitat. Isolated habitats (e.g. sandflat reef) along with areas characterized by less structural complexity (e.g. marsh – sand interface) were among the least preferred areas in this study. Variation in habitat selectivity among the different oyster reef classifications corroborated our consensus that landscape setting of individual habitat classifications, rather than overall availability, has a greater influence on habitat selection by red drum in this study.

A major challenge with evaluation of habitat value involves the capacity for generalizing ecological processes and function across broader spatial and temporal gradients (Bostrom et al. 2011). The influence of habitat complexity and connectivity on species assemblages within the seascape is well recognized in estuarine systems (Micheli and Peterson 1999, Sheaves 2009, Kenworthy et al. 2018). The results from our study corroborate these findings as red drum selected for areas of the seascape where multiple habitats converged (i.e., saltmarsh, oyster reef, and seagrass). In a similar study Dance and Rooker (2015) revealed preference for highly complex and well connected habitats within the seascape, although their data suggested a greater selection for seagrass over oyster reef habitats. In this Texas estuary, seagrass was generally the

more abundant habitat directly proximate to saltmarsh while in our study oyster reef was most abundant. Complexity and connectivity associated with saltmarsh habitat thus may be more of a suitable predictor of habitat selection by red drum rather than habitat identity or complexity alone. In fact, we also observed increased fish positions at the interface of marshes along the norther and western boundary of the study are which contained more seagrass than oyster reef directly proximate to the salt marsh interface. Furthermore, we did not observe notable enhancement of fish activity at seagrass reefs where two high structured habitats converge, further corroborating the hypothesis that saltmarsh is a focal habitat feature within seascapes whereas the apparent value of alternative habitat classifications depends on their proximity to this habitat.

Distinguishable within habitat differences in resource utilization among oyster reefs highlights the need to consider spatial context when examining ecosystem services provided by this habitat classification. Distinct location specific responses by red drum in this study counter previous assertions that resource selection at the scale of this study embayment would result in equal selection for the same habitat classification by transient fish regardless of its location within the overall seascape (Keller et al. accepted). Whereas stakeholders commonly assume universal value and function of oyster reef habitat regardless of location within the environment, these results corroborate previous research suggesting that delivery of ecosystem services do vary significantly within a small area (e.g. the extent of this embayment) (Micheli and Peterson 1999, Grabowski et al. 2005, Ziegler et al. 2018). These results are particularly influential for developing specific goals and objectives within oyster restoration initiatives (Bagget et al. 2015). The generality of these results across a variety of fish species, particularly those that are less transient, deserves further research attention.

Linkages between habitat use and distribution of preferred dietary resources are well documented for a range of fish species and habitats (Rozas and Odum 1988, Lowe et al. 2003, Wenger et al. 2018). Red drum could potentially be selecting these high complexity landscapes to maximize foraging opportunities on blue crabs and small fish, which are known to occur at greater densities in highly connected estuarine environments (Summerson and Peterson 1984, Irlandi and Crawford 1997, Micheli and Peterson 1999). Interestingly though, we also observed a slight increase in selection for seagrass coinciding with a reduction in selectivity for reef habitat as the study progressed from summer into fall. Changes in the configuration and complexity of seagrass associated with senescence of *Zostera* through the study may explain the shifting selectivity. Red drum were likely less efficient at acquiring preferred prey (i.e. blue crabs) in large dense seagrass meadows during summer; whereas small patchy meadows during the fall potentially facilitated foraging success and notable shifts in habitat preferences (Mahoney et al. 2018). Contrasting these observations however is that red drum did not respond positively to densities of crustaceans, particularly xanthid crabs, which previous studies have demonstrated occur in greater densities at sandflat reefs in this seascape (Grabowski et al. 2005, Ziegler et al. 2018). These data highlight the need for more quantitative understanding of habitat associations across broader spatial and temporal gradients and their implications for shaping food web dynamics in estuarine seascapes.

Intuitively, we assume that an individual's need for food and shelter amidst pressure from predation and competition is reflected in their resource selection behavior (Resettarits 2005). Fine scale resolution monitoring of red drum behavior revealed insightful knowledge of within habitat and landscape-specific habitat use over time, although interpreting process (i.e. foraging, fleeing predators, resting, transiting ...) from pattern (spatiotemporal distribution of fish positions) is

often challenging using telemetry data. For instance, selection indices identified sand to be the least preferred habitat in this embayment. Examination of individual fish tracks generally suggested a transiting behavior (identified by straight line paths) rather than foraging (consistent changes in movement direction) when fish positions were within sand habitat. Conversely, results from a hook and line survey from a companion study within this same embayment suggested foraging activity occurred among sand habitats located away from structured oyster reefs (Ziegler et al. 2018). While we evaluated habitat use in terms of positions within each habitat, inference of behavior requires examination of positions through time at a greater resolution. Manual inspection of several fish tracks identified repeated visits to saltmarsh reefs within this embayment. Presumably this activity reflects foraging behavior, although these assumptions would require additional attention. Furthermore, while the halo habitat appeared to be highly selected for in this study, closer observation of detailed fish tracks suggested that this area of the seascape was used more as a corridor for fish transiting parallel to the marsh interface. Apparent selection for this habitat may in reality be due to its proximity to the saltmarsh interface rather than active selection for some ecological benefit.

The data collected in this study advance our understanding of habitat associations for a common estuarine fish species within a complex estuarine seascape. As has been highlighted, there are limitations in our capacity to extrapolate these observations across broader spatial scales and broader ecological implications (e.g., specific behaviors). Future utilization of the analytical approaches employed in this study could be substantially enhanced if used in conjunction with additional sampling gears and techniques (Kenworthy et al. in Prep). For example, incorporation of stable isotope data for red drum within this system could potentially help resolve the discrepancies in habitat selectivity over time among the seagrass and oyster reef

habitats to better understand food web dynamics. The general assumptions regarding association with high habitat complexity and connectivity need to be examined in additional seascapes. Red drum occupy a range of habitats within estuarine systems, many which do not contain high abundances of oyster reef habitat. While oyster reef was highly valued in this study, habitat associations will likely vary among various seascapes. Overall, these data provide a better understanding of habitat associations for red drum in this temperate estuarine seascape at a much greater resolution highlighting the need for evaluating the value and function of estuarine habitats across the entire seascape rather than focusing on limited areas (Nagelkerken et al. 2015).

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TABLES

Table 2.1 Summary of 34 red drum tagged with acoustic transmitters and tracked within the LOTEK fine scale positioning array within Middle Marsh in central North Carolina.

Fish ID	Release Date	Total Length (mm)	Weight (kg)	Total Detections	Days Detected
RD01	2011-07-13	488	1.1	0	0
RD02	2011-07-14	490	1.3	0	0
RD03	2011-07-14	490	1.4	175	1
RD04	2011-07-14	480	1.1	6727	25
RD05	2011-07-15	514	1.6	0	0
RD06	2011-07-15	515	1.5	8337	2
RD07	2011-07-15	503	1.3	0	0
RD08	2011-08-16	559	2	1126	2
RD09	2011-08-16	520	1.6	35511	24
RD10	2011-08-16	365	0.6	2636	7
RD11	2011-08-16	505	1	549	2
RD12	2011-08-16	340	0.6	38	1
RD13	2011-09-03	565	2	11598	23
RD14	2011-09-03	341	0.6	2148	2
RD15	2011-09-13	775	4	4729	9
RD16	2011-09-13	755	4.5	0	0
RD17	2011-09-13	549	1.6	1158	3
RD18	2011-09-30	563	1.6	951	3
RD19	2011-09-30	556	1.5	9120	37
RD20	2011-09-30	568	2	123	3
RD21	2011-09-30	600	2.3	487	1
RD22	2011-10-04	610	2.2	16585	29
RD23	2011-10-04	562	1.6	840	2
RD24	2011-10-04	645	2.6	22	2
RD25	2011-10-04	612	2.3	952	4
RD26	2011-10-04	585	1.9	33	2
RD27	2011-10-06	600	2	7593	7
RD28	2011-10-06	612	2.3	8096	10
RD29	2011-10-06	556	1.6	0	0
RD30	2011-10-06	638	2.8	5144	4
RD31	2011-10-06	555	1.5	2871	5
RD32	2011-10-10	550	1.6	870	6
RD33	2011-10-10	602	2.2	15901	22
RD34	2011-10-10	534	1.5	0	0

Table 2.2 Summary of the total number of detections for all fish within each habitat classification during the early, middle, and late time periods. Values in parentheses identify proportion of positions for each habitat classification during each time period.

Habitat	Early	Middle	Late
Seagrass	14920 (39.7 %)	27842 (38.7 %)	16494 (47.5 %)
Sand	5559 (14.8 %)	17636 (24.5 %)	10205 (29.4%)
Halo	10016 (26.6 %)	13611 (18.9 %)	5008 (14.4%)
Marsh	42 (0.1 %)	359 (0.5 %)	67 (0.2 %)
Sandflat Reef	32 (0.1 %)	537 (0.7 %)	9 (< 0.1 %)
Seagrass Reef	722 (1.9 %)	1340 (1.9 %)	19 (0.1 %)
Marsh Reef	2223 (5.9 %)	5000 (6.9 %)	1462 (4.2 %)
Fringe Reef	4082 (10.9 %)	5662 (7.9 %)	1473 (4.2 %)
Reefs Combined	7059 (18.8 %)	12539 (17.4 %)	2963 (8.5 %)

Table 2.3 Summary of habitat availability represented as percent of individual classifications during each time period.

Habitat	Early	Middle	Late
Seagrass	43.00	27.50	26.00
Sand	50.40	65.60	67.00
Halo	2.90	3.10	3.20
Marsh	0.50	0.50	0.51
Sandflat Reef	0.10	0.10	0.10
Seagrass Reef	0.10	0.10	0.10
Marsh Reef	0.80	0.80	0.80
Fringe Reef	2.20	2.30	2.30
Reefs Combined	3.20	3.30	3.30

FIGURES

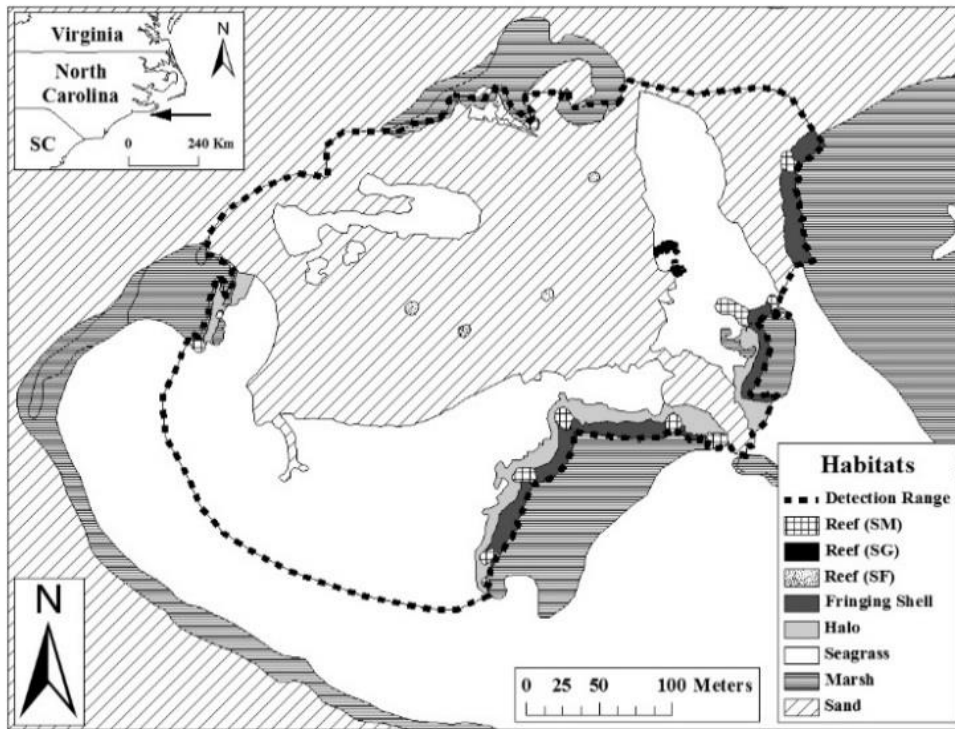


Figure 2.1 Distribution of habitat types within the acoustic detection arena at our study site in Middle Marsh, North Carolina. In addition to sand, halo, seagrass and marsh habitats, the study area contained oyster reef habitat across multiple landscape contexts. This example map depicts seagrass cover during the early period of the study (July 15 – August 31) before the seasonal loss of above ground biomass.

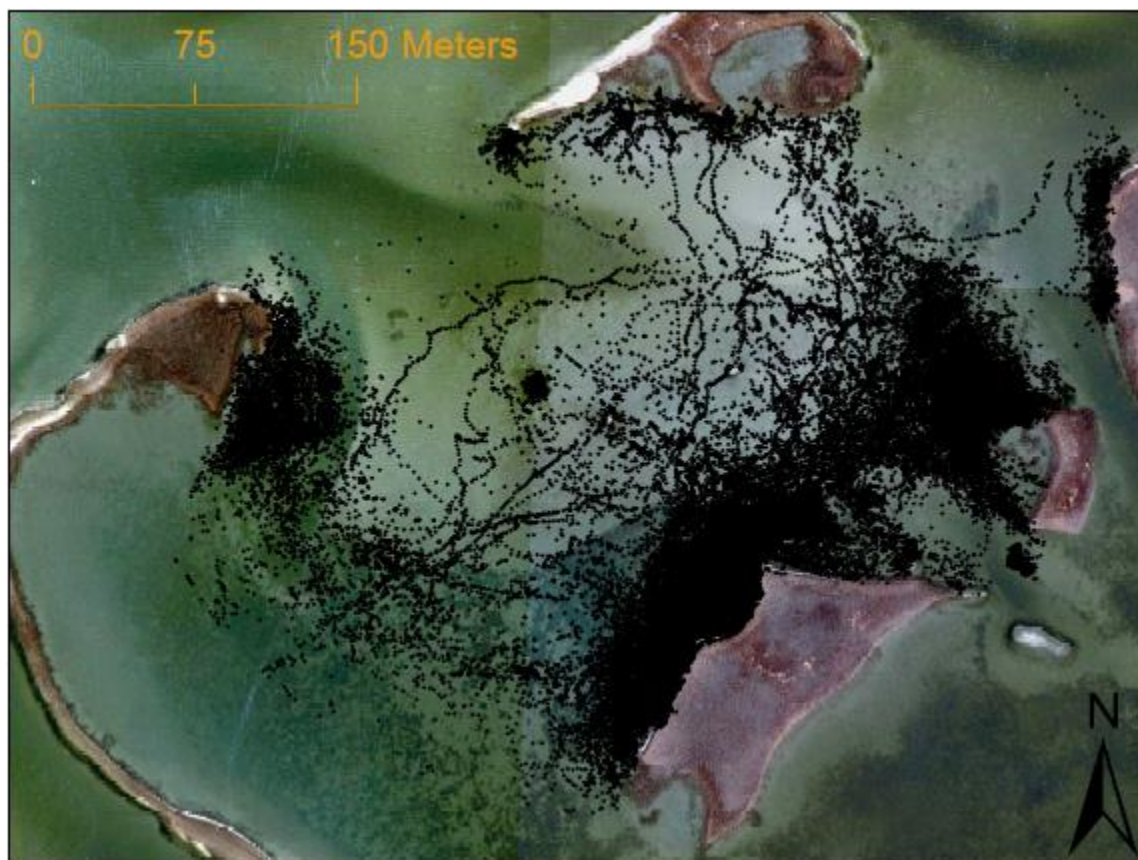


Figure 2.2 Relocations of all fish throughout the entire study superimposed on an aerial image of the study site. Each black dot represents an individual position.

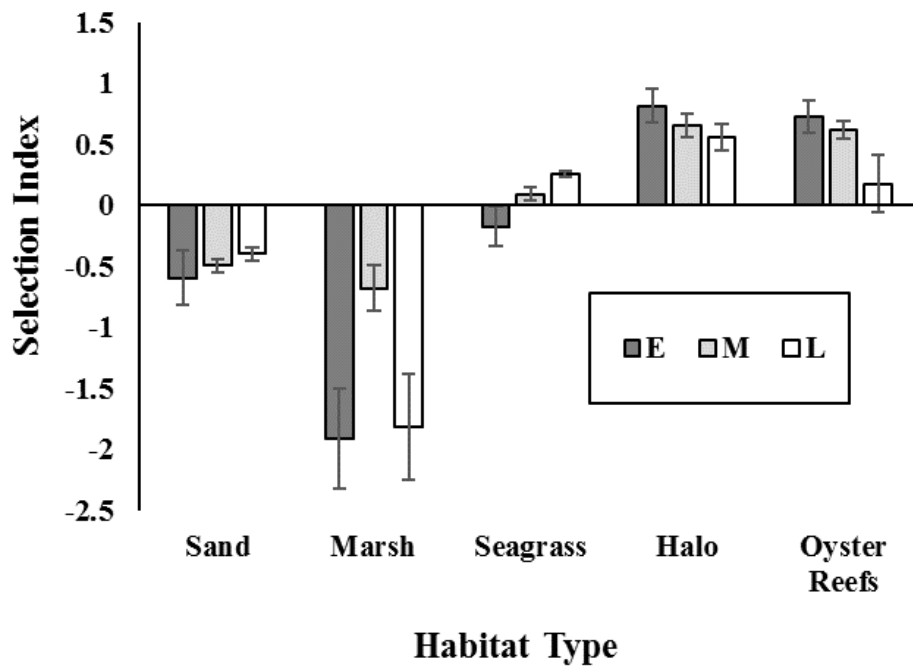


Figure 2.3 Habitat preference of red drum detected during the early (E), middle (M), and late (L) periods. Shown are the mean $\pm$ 1 standard error for each habitat classification during respective time periods. The ‘Oyster Reefs’ classification identifies selection indices for all individual reef classifications combined. Values above the zero line indicate general preference for individual habitat classifications while values below represent general avoidance of respective habitat.

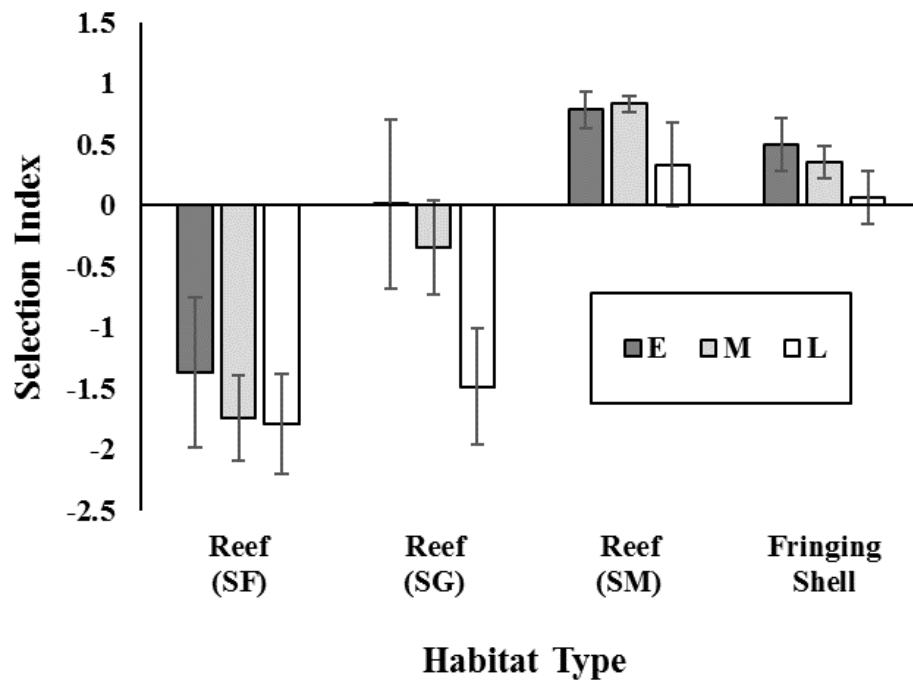


Figure 2.4 Habitat preference of red drum detected during the early (E), middle (M), and late (L) periods. Shown are the mean $\pm$ 1 standard error for each oyster reef classification during respective time periods. Values above the zero line indicate general preference for individual habitat classifications while values below represent general avoidance of respective habitat.

CHAPTER 3: COMPARING ACOUSTIC TELEMETRY AND TRADITIONAL GEARS TO MAXIMIZE SPATIOTEMPORAL RESOLUTION IN ESTUARINE FISH RESEARCH AT INDIVIDUAL, SPECIES. AND COMMUNITY LEVELS

Introduction

Comprehensive assessments of the spatial ecology of marine fish populations are fundamental to developing effective management and conservation strategies for ecologically and economically valued species. Key to accomplishing this is generating an accurate assessment of the spatiotemporal trends in distribution, abundance, and behavior of fish species (Murphy and Jenkins 2010). Obtaining data necessary to accomplish these goals and objectives is particularly challenging in estuarine environments where a number of biotic (i.e. foraging and reproductive behaviors) and abiotic (i.e. temperature, salinity, and dissolved oxygen) processes are influencing movement and behavior of individuals within the population (Sheaves 2016). Whereas, management strategies often rely on spatiotemporal dynamics of species abundances and distribution (i.e. catch rates) and demographic parameters (i.e. natural mortality, population age, size and sex structure, and growth) to inform conservation initiatives; greater attention to ecosystem-based management strategies has generated increasing interest in quantifying fish habitat relationships, habitat quality and quantity, and human impacts on fish populations (Botsford et al. 1997, Browman et al. 2004, Curtin and Prellezo 2010). New sampling techniques and analytical tools continue to be applied in studies evaluating the spatial ecology of fishes in nearly all aquatic environments worldwide. Thus, it is essential that ecologist and managers fully

understand the characteristics of data being collected to ensure efficient development of conservation initiatives.

Fundamental to documenting the spatial ecology of fish in estuarine environments is the ability to directly capture or observe individuals at representative spatial and temporal scales. Researchers have employed a variety of tools, techniques, and gears to examine the spatial ecology of fish in shallow estuarine systems. Historically, data collection has been accomplished using a variety of “traditional” gear types including towed nets (e.g. trawls and seines), passive samplers (e.g. gill-nets, channel nets, and fyke nets, gee traps, pots, hook and line), and enclosure samplers (e.g. purse seine, drop net, throw trap, and lift net) (Rozas and Minello 1997). Alternative methods such as diver-based surveys and baited remote underwater video have also been used to observe fish directly; however, these tools have limited applicability in most estuarine systems due to high turbidity (Taylor et al. 2013). Using traditional gears the spatial ecology of fishes is evaluated using standardized catch per unit effort (CPUE) data across spatial and temporal gradients. Spatiotemporal CPUE data has underpinned estuarine fish management strategies since the late 19th century, but researchers have recently acknowledged some shortcomings associated with sampling using these gears (i.e., size and species selectivity, spatial limitation, infrequent sampling, among others) (Olin and Malinen 2003, Hubert et al. 2012).

Over the broad history of fisheries research, technological advancements have provided researchers with new tools to monitor fishes in their environment (Cook et al. 2044). Specifically, acoustic telemetry (hereafter referred to as telemetry) allows researchers to monitor the activity of individual fish equipped with electronic tags. Fishes can either be tracked actively, using a vessel to follow individuals, or passively using autonomous receivers deployed in predefined configurations. Over the last ~20 years, there has been a significant increase in the

number of studies using telemetry to monitor the spatial ecology of estuarine fish. A Web of Science search using the term “acoustic telemetry” identified an increase in the number of publications from nine in 2000 to over 100 each in 2015, 2016, and 2017) (e.g. Capello et al. 2015, Crossin et al. 2017, Taylor et al. 2017). Despite the increasing popularity of this technology to sample fish populations, many research programs continue to use traditional sampling gears alone or in conjunction with other tools. The introduction of telemetry has undoubtedly yielded more insight into the spatial ecology of fish in estuarine environments (Cook et al. 2004, Meyer 2017), but the technique may still be underutilized or not used optimally in conjunction with other gears and analytical techniques because researchers do not have a firm understanding of the advantages and limitations of the different sampling gears available.

With a growing number of individuals, agencies, organizations, and nations demanding more scientific knowledge regarding the ecology of fish species, it is imperative that researchers are effectively utilizing available resources in data collection efforts. In this review, we compiled and synthesized the scientific literature to compare the application and suitability of sampling designs using telemetry versus traditional gears in research designed to quantify the spatial ecology of estuarine fishes. We focused our review of the traditional gears on gill-nets and trawls because of the frequency that these two gears are used. Our objectives were to: 1) characterize the recent trends in research topics addressed using each gear type; 2) summarize the quantitative characteristics of data collections and costs associated with each gear type; and, 3) compare the results from two case studies which utilized both traditional gears and telemetry data to explore the same research questions (from the same location). Overall, the information outlined in this

review can provide guidance to researchers in planning and implementing new research examining the spatial ecology of estuarine fish.

Methods

Literature Search

We limited our analysis to research conducted in estuarine waters of the USA and Canada. To compare characteristics of sampling fish using gill-nets, trawls, and telemetry, we identified a representative sample of studies that used at least one of these gear types in their sampling design. Publications were identified using an ISI Web of Science search with the following combination of search terms: “acoustic telemetry” and “marine” and “fish”; “gill-net” and “fishes”; “gill-net” and “estuary”; “trawl” and “fishes”; “trawl” and “estuary” and “fishes”; and “trawl” and “estuary”. We included “marine” as a search term with telemetry due to the large volume of publications (n = 198) returned for a search with just “acoustic telemetry” and “fishes”. Likewise, “estuary” was paired with “trawl” and “fishes” due to the number of publications (n=500) with the two terms alone. Because we wanted to identify recent trends in how these gears are being used in research, we limited our search to studies published from January 2013 through July 2018. Studies on anadromous species were included in our analysis provided a component of the sampling design occurred within estuarine environments. Publications from the above Web of Science searches were screened to identify studies that reported on key metrics (see data collection metrics below) which allowed us to compare the nature and efficacy of one/both sampling approaches. Due to the quantity of telemetry studies (n = 43) remaining, we selected a subset of papers identified by the first twenty-eight from the list of publications sorted alphabetically by author.

Research Topics

We identified the major research topics addressed for each study identifying 13 major themes among the selected publication. Using a vote-counting procedure we identified how many papers addressed each research topic. Because studies often address a variety of questions and objectives, multiple topics could be associated with a single study. To compare total number of topics and frequency of them occurring in studies using each gear type, we generated a frequency matrix identifying the proportion of studies addressing each topic for each gear. The major topics included: habitat selectivity (e.g. habitat choice, home range, core area, activity space, etc.), population dynamics (e.g., survival, recruitment, growth), community dynamics (e.g. species composition, richness, diversity, etc.), movement parameters (rates, timing, frequency, residency, etc.), connectivity, spawning behavior, responses to abiotic conditions, spatiotemporal abundance (spatiotemporal changes in relative abundance and distribution), population contingents, foraging dynamics, individuality, edge effects, and range expansion.

Data Collection Characteristics

We explored the scope of sampling effort for each study by quantifying several metrics comparing among gear types. Most of the publications provided adequate information to quantify all of the data collection metrics (Table 3.1). Instances for which we were unable to quantify a metric were typically limited to one per publication and were not common among all the publications. Therefore, we felt that the means and ranges quantified in this review adequately represented the metrics explored. First, we wanted to identify similarities and differences in the quantity and size of fish sampled using each gear type. We extracted the reported number of species studied (Species Count), quantity of fish studied (Fish Count), and mean size of individuals studied (Average Fish Size) for each publication.

Next, we defined the spatial extent (Coverage Area) of active sampling within each study. This metric identified the area around each gear type where detectability of target animals was greatest. For acoustic telemetry research, this was quantified as the area of a circle with the hydrophone in the middle and radius equal to the reported detection range of the transmitters deployed in the study. The total area monitored in the study was then quantified by multiplying the single hydrophone sampling area by the number of hydrophones deployed. For hydrophone arrays with overlapping detection ranges, we removed the estimated area of overlap from the final calculations of area monitored. For gill-nets, the capability of identifying the presence of a fish only occurs when a fish physically gets entangled in the gear. For quantifying the area monitored by gill-nets, we assumed that the area actively sampled by a net is equal to the area where fish experience a nearly 100% probability of encountering and becoming entangled in the net. Although the probability of encounter varies according to species- and size-specific swimming speed, length of net, and soak time, the 100% probability remains highly confined to the area directly adjacent to the net (Griffiths et al. 2006). Because exact quantification of this distance from the net would be challenging for each study, we assumed a standardized distance of five meters when calculating the area monitored in gill-net studies. Therefore, total area monitored per net was quantified as the area of the rectangle with length equal to the distance of net deployed and a width of ten meters (five meters on either side of the net). The total area monitored in each study was determined by multiplying the sampling area per net by the total number of nets deployed in the study. We quantified the area monitored for trawl studies by multiplying the width of the trawl used by the tow length. When tow distance was not listed directly in the publication, these values were calculated based on reported average tow speeds and duration.

Finally, we explored temporal sampling characteristics of each gear by quantifying the duration (Study Duration) and active sampling time (Monitoring Effort) for each study. Study duration was identified as the length of time from the start (release of first tagged fish for telemetry studies and deployment of first net for traditional gear) to the end (removal of hydrophones for telemetry studies and retrieval of last net for traditional gear) of the study. For telemetry studies, removal of hydrophones typically coincided with estimated life of transmitters used in the study. Monitoring effort for each study was quantified as the amount of time each gear type was actively in the water sampling over the duration of the study. For telemetry studies, this was identified as the proportion of time hydrophones were in the water when tagged fish were in the system (i.e. from the point when the first tagged fish was released until the end of the study). Monitoring effort for the traditional gear was identified as the proportion of time the gear was actively sampling over the duration of the study. For gill-nets, active sampling was considered the cumulative amount of time that nets were in the water. Nets deployed at the same time, regardless of location, were considered one event because temporal effort was the same for each net. Total soak time for each gill-net study was equal to the sum of individual event soak times. Finally, total sampling effort for trawl surveys was calculated by multiplying the average tow time by the total number of tows conducted for each study. Comparisons among the gear types were carried out by exploring means and ranges of each metric quantified.

Case Studies

The literature-based data provides a valuable overview of the trends in recent research and a review of how different gears are currently being used; however, this exercise provides less opportunity to directly compare these gears side by side and address whether these approaches corroborate one another when applied in tandem to the same question. Here we present two case

studies where both traditional gear and acoustic telemetry were used to explore the same research questions and objectives. The first case study (further referred to as ‘fine-scale habitat-selectivity case study’) explored the role of restored oyster reefs as essential habitat for red drum (*Sciaenops ocellatus*). The study site was in a small (100,000 m²) semi-enclosed marsh embayment located in the Rachel Carson National Estuarine Research Reserve near Beaufort, North Carolina (Fig. 3.1). The embayment contained six restored intertidal reefs, formed by the eastern oyster (*Crassostrea virginica*), in three separate landscape settings (on a mud flat, adjacent to saltmarsh, and adjacent to seagrass). Reefs were originally constructed as part of a restoration study in 1997 (described fully in Grabowski et al. 2005) and later revisited to monitor the nekton abundance 13 years post-construction (Ziegler et al. 2017). Nekton were collected using gill-nets (10 m long X 1.5 m tall; 7.62 cm stretch mesh) at the restored reefs (n = 6) and non-reef control sites (n = 6) monthly between July 2010 and November 2010. Using these catch data, we quantified the delta density (sensu Serafy et al. 2007) for red drum at each of the restored reefs and control sites. The delta density index is considered a better estimate of relative density for data sets characterized by inflated variance due to large quantities of zero values. Due to low catches of red drum at these locations, we also explored the cumulative response of a mixture of piscivorous fish including Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), pigfish (*Orthopristis chrysoptera*), flounder species (*Paralichthys albiguttata* and *Paralichthys lethostigma*), bluefish (*Pomatomus saltatrix*), spot (*Leiostomus xanthurus*), black drum (*Pogonias cromis*), and red drum (*Sciaenops ocellatus*) which are often associated with these target habitats in the embayment. During the following summer/fall season (July 2011 – November 2011), we monitored habitat selectivity of acoustically tagged sub-adult red drum (550 ±15 mm total length [TL], mean ± 1 standard error [SE]) (n=34) in this same embayment using a high-resolution

tracking system (LOTEK Inc. MAP 600) (described fully in Fodrie et al. 2015). Sub-meter accuracy positioning of fish was used to quantify detection activity at the same restored oyster reef and control habitats monitored with gill-nets the previous season. We compared the trends in habitat selectivity between the two gear types by generating bar plots for delta density (gill-nets) and detection densities (acoustic telemetry).

In the second case study (further referred to as estuarine-scale seasonal distribution case study) we explored the spatiotemporal distribution of red drum and black drum (*Pogonias cromis*) within the New River Estuary (NRE) in North Carolina. Using fisheries independent gill-net survey catch data collected by the North Carolina Division of Marine Fisheries, we quantified quarterly CPUE (delta densities) for both species within the upper, middle, and lower portions of the NRE from August 2012 through December 2015 to coincide with the telemetry study below (Fig. 3.1). Through a stratified random sampling design, the NRE was sampled once in February and December months, but twice monthly in all other months using two experimental gill-nets (one each at a deep and shallow site) during each sampling event. Experimental gill-nets were comprised of eight 27.4 m segments of 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, 15.2, and 16.5 cm stretch mesh. At the shallow site, each of the eight segments were set individually perpendicular to shore while at the deep location all segments were set attached to each other in a single line. Starting in August 2012 sub-adult red drum (529 ± 12 mm TL) ($n = 55$) and sub-adult black drum (455 ± 05 mm TL) ($n = 36$) were acoustically tagged and released from a variety of locations within the NRE. Fish distribution was monitored using forty-five VEMCO VR2W hydrophones deployed throughout the NRE. To identify distribution patterns of tagged fish, we quantified residency indices by dividing the number of days each fish was detected by the total number of days each fish was monitored (sensu Daly et al. 2014). Using

detection patterns at hydrophone gates located at entry/exit points into the NRE, we estimated the total number of days each fish was in the NRE. Residency indices were calculated separately for each season and region of the river. This method standardized detection data for each fish regardless of the total time the individual was in the system by providing a value ranging from 0 (fish detected zero days while in the system) to 1 (fish detected every day while in the system). Like the fine-scale habitat selectivity study, we compared trends in spatiotemporal distribution identified with the two gear types by generating bar plots of delta density (gill-nets) and residency indices (acoustic telemetry). To prevent any potential size bias in our comparison of the two gear types, red drum and black drum caught in the gill-net survey that were smaller than the minimum sizes monitored in the telemetry study were not included in the analysis.

Cost Analysis

Using the sampling designs presented in the two cased studies above, we developed a gear-cost analysis. Because certain variables can vary significantly among research programs (e.g. salaries, project overhead, and field time), this analysis focused primarily on the direct gear costs. Cost calculations presumed that none of the required equipment was already owned by the research group at the commencement of each study. Although this belies the leveraging of equipment by research groups, studies do not typically report the source(s) of gear. Cost projections in this analysis thus are most useful for researcher groups starting telemetry studies from scratch. Unit prices used in this analysis reflected price quotes obtained by the authors from Memphis Net and Twine (gill-nets), VEMCO (acoustic telemetry), and a local hardware store (hydrophone moorings) for similar research conducted in the past five years. Gill-net costs included the purchase of new nets, including foamcore float line and leadcore sinking line, as well as surface floats for each net. Because damage to gill-nets is inevitable, we included costs to

repair each net once every six months. Replacement cost estimation assumed research groups would hang new netting with the original float line, lead line, and marker floats, therefore price estimates for repair reflect the cost of replacement mesh only. Acoustic telemetry costs included the purchase of hydrophones, transmitters, and supplies for constructing moorings for each hydrophone. The equipment used for fish tracking in the fine-scale habitat selectivity study is no longer being manufactured, therefore we calculated costs to conduct this study using the VEMCO Positioning System (VPS). Replacement gear for the acoustic telemetry studies assumed a 10% hydrophone loss rate. Replacement estimates for both gear types reflected the experience of the authors conducting similar research.

Results

Research Topics

A total of 57 publications were examined that utilized acoustic telemetry (n=28), gill-nets (n=16), or trawls (n=13) to sample the distribution of estuarine fishes in the USA and Canada within the past 5 years (Table 3.1). Telemetry studies covered a greater number of research topics (n=9 topics) compared to studies using gill-nets (n=6) and trawls (n=5); although comparisons per total number of papers (i.e., topics/paper) indicates a greater diversity of research topics addressed in studies using gill-net (0.37) and trawls (0.38) compared to telemetry (0.32) (Table 3.2). Of the sixteen research topics identified across studies, just two (habitat selectivity and responses to abiotic conditions) were explored using all three gears. Furthermore, only three other topics (i.e. survival, community dynamics, and population dynamics) were studied using at least two of the gear types. Habitat selectivity was the most commonly explored topic for research using acoustic telemetry (36% of studies) and gill-nets (50% of studies), while

community dynamics was the most commonly explored topic in studies using trawls (62% of studies).

Data Collection Characteristics

Overall, the number of individual fish sampled with trawls was greatest among the gears explored (Table 3.3). Mean species counts for trawl studies (36.4 ± 12.0 species; mean $\pm$ SE) were four times greater than gill-net studies (8.4 ± 3.4 species) and more than an order of magnitude greater than acoustic telemetry studies (1.3 ± 0.2 species). The minimum species count for all gears was identical among all gear types (one species) while the maximum number of species increased from five in telemetry studies to 51 and 114 in gill-net and trawl studies, respectively. Mean number of fishes sampled per study followed the same general trend as species counts, with trawl studies ($36,948 \pm 31,463$ fish) sampling one to two orders of magnitude more fish on average compared to gill-net ($2,087 \pm 851$ fish) and acoustic telemetry (156 ± 68 fish) studies, respectively. Mean fish size in studies using gill nets (844 ± 184 mm TL) was more than double the average size observed in acoustic telemetry studies (395 ± 44 mm TL) and almost six times larger than the average size observed in trawl studies (145 ± 35 mm TL). In addition to the greatest mean fish size, gill-net studies (322 – 2611 mm TL) also sampled the greatest range in fish size. Whereas there was no overlap in size range between gill-net studies and trawl studies (35 – 300 mm TL), the range in fish size for telemetry research (46 – 920 mm TL) overlapped with the ranges for each of the other gears.

Acoustic telemetry studies sampled larger areas than studies using the other two gears. The average area sampled per study for acoustic telemetry research (16.0 ± 6.9 km²) was 50-60% greater than gill-net (7.9 ± 3.6 km²) and trawl (9.6 ± 8.4 km²) studies. Although acoustic telemetry studies sampled the largest areas, they were the shortest in duration (587 ± 86 days).

Average duration of trawl ($1,970 \pm 536$ days) and gill-net ($3,804 \pm 1,146$ days) studies were more than double the average duration of acoustic telemetry research. Although telemetry studies were on average the shortest in duration, the proportion of time the gear was actively sampling fish (0.62 ± 0.08) was three and four orders of magnitude greater than studies using gill-nets (0.06 ± 0.02) and trawls (0.005 ± 0.002), respectively.

Case Studies

In the fine-scale habitat-selectivity case study, red drum were only captured at the seagrass and saltmarsh control sites and CPUE was two times in the seagrass landscape compared to the saltmarsh landscape (Fig. 3.2A). Considering overall red drum catch rates were extremely low ($n = 3$), delineating any convincing patterns was not possible. Catch rates of all piscivorous fishes ($n = 50$ individuals captured) were also highest in the seagrass landscape compared to saltmarsh and mud flat landscapes regardless of reef presence (Fig. 3.2B). Catch rates for piscivorous fishes were 1.4 and 3.8 times greater at control sites compared to reef sites for seagrass and mud flat landscapes respectively. Detection activity from the fine-scale tracking study indicated different patterns in habitat use compared to piscivorous fish catch data from the gill-net survey (Fig. 3.2C). Detection activity was more than double at the restored reefs compared to the control sites for all landscapes combined. Only the detection patterns in the saltmarsh landscape reflected general patterns observed in the gill-net catch data with greater activity at the control sites compared with the restored reefs.

In the estuarine-scale seasonal distribution case study, the long-term gill-net survey and the telemetry data were relatively consistent in predicting the distribution of red drum and black drum in the NRE. Red drum delta density quantified from gill-net CPUE for during spring months were relatively even within all regions of the NRE (Fig. 3.3A). Red drum delta density

during summer and fall was approximately 2x and 1.7x greater respectively in the lower region of the NRE compared with both the middle and upper regions. Delta densities during the winter months were relatively low with minimal differences among the regions of the NRE. Residency indices quantified in the telemetry study were consistent with gill-net survey distribution patterns during the spring and summer months; however, discrepancies between the two gears were observed in the fall and winter months (Fig. 3.3B). Residency indices during the fall months indicated a more even distribution of fish between the lower and middle region of the NRE compared with the gill-net survey. Additionally, delta densities indicated an increase in activity with distance up the NRE in the winter months, whereas residency indices only showed this pattern between the lower and middle regions with almost no activity occurring in the upper region.

Black drum catches from the gill-net survey during spring months indicated highest delta densities in the lower region of the NRE (1.5 times greater) compared with both the middle and upper regions (Fig 3.3C). During the summer months, this pattern was different as densities were considerably greater in the middle region compared with the lower (two times greater) and upper (eight times greater) regions. Fall delta density patterns indicated a decrease in fish presence with distance up the estuary and during winter months, black drum were only captured in the lower region of the NRE. Contrary to results from the gill-net survey, the telemetry data suggested that black drum activity was highest in the middle region during spring and fall months whereas gill net data suggested activity was greater in the lower region (Fig. 3.3D). Telemetry data for the summer and winter months, however were consistent with gill net-net survey indicating highest activity in the middle region during summer months and lower region during winter months.

Evaluation of the prices for equipment needed to conduct each case studies indicated greater costs for both of the telemetry studies ((\$27,870 and \$105,530) compared with the two gill-net based studies (\$731.80 and \$2,332.90) (Table 3.4). Interestingly, the cost ratio for the gill-net approach compared to the telemetry approach for each case study was approximately equal (2.5% and 2.2% respectively). In addition to the notably greater cost for primary sampling gear (e.g. the hydrophones and the nets themselves), telemetry studies had more accessory gear and costs associated with the study. For example, the telemetry studies require moorings to connect the hydrophones too. Additionally, in the fine-scale habitat-use case study, additional reference tags and data analysis are required which added on additional costs (~\$3,060).

Discussion

Our synthesis highlights several ways in which multiple gear types are utilized in ecological research evaluating the spatial ecology of estuarine fish species. Our comparison of major research themes addressed in recent studies indicated some overlap in research topics (e.g. habitat selection and species distributions) whereas there was little overlap in other areas of research such as movement parameters for individuals (primarily studied using telemetry) and community dynamics (primarily studied using traditional gear). The differences in research topics addressed can be linked to the sampling characteristics associated with each gear type. For example, this review demonstrates that researchers are capable of sampling with greater spatial and temporal resolution using telemetry which is necessary for identifying high resolution fish behavior (e.g., movement parameters) and spatiotemporal distribution for individuals. Additionally, because traditional gears sample a greater quantity and variety of individuals and species, they have been utilized primarily in studies evaluating community based research

questions. Overall, the patterns that have emerged from this review provide guidance on the advantages and limitation of using telemetry and traditional gears to address research needs aimed at influencing management decisions.

Surprisingly, there was little overlap of research topics between gear types which is indicative of both the benefits and limitations associated with using telemetry in fish ecology research. Although telemetry was used to address a greater variety of research topics in this review, these patterns are likely highlighting a shift in gear choice. Nonetheless, greater resolution of animal behavior has promoted several new opportunities for research (i.e. individuality and population contingents). The greater variety of topics examined using telemetry reflects the added capacity to quantify behavior of individual fish in wild settings. The increased focus on individual level behavior of fish however has also been a factor limiting the relevancy of telemetry data in fisheries management programs (Crossin et al. 2017). Scaling up animal behavior from the individual level in a localized area to the entire population and community remains challenging (Schick 2008). Community and population level research continues to be conducted using traditional gears designed to identify large-scale patterns of distribution and abundance over time (i.e. long-term fisheries independent surveys). Efforts have been made to quantify community level interactions using telemetry approaches to monitor large quantities of species on coral reefs (*sensu* Kendall et al. 2017), although similar efforts are lacking in estuarine research.

Telemetry technology covers a significantly greater area in field studies thus increasing the probability of detecting target animals within sampling locations. While the sampling area of gill-nets or trawls is restricted by the length of net or distance towed, respectively, telemetry hydrophones are capable of detecting telemetered fish at greater distances (*sensu* Gahagen et al.

2015), significantly increasing the area monitored per individual gear set. This is particularly beneficial for studies needing to quantify the presence/absence of individuals in relatively open areas (i.e., large scale movement parameters, connectivity, and response to abiotic conditions) or requiring reliable detection of individuals emigrating from a specific location (i.e. residency and survival studies). Enhanced abilities to detect fish from great distances, however can also inhibit accuracy in quantifying habitat selectivity if target habitats are only a small fraction of the overall detection area of the hydrophone (i.e. fine-scale habitat selectivity). These research needs can be resolved using fine-scale tracking sampling designs (sensu the fine-scale habitat-selectivity case study we evaluated) or by using active tracking approaches (Ahr et al. 2015, Farris et al. 2016, Freedman et al. 2016 Lowerre-Barbieri et al. 2016, Friedle et al. 2013).

In addition to greater spatial coverage, telemetry alleviates concerns of limited temporal resolution associated with traditional gears through continuous monitoring of target fish. Variability in fish movement and distribution can occur as a result of environmental conditions (Bell et al. 2003), food availability (Cunjak et al. 2005), predation pressures (Hammerschlag et al. 2010), spawning activity (Young et al. 2014), time of day (Luo et al. 2009), and season (Wingate and Secor 2011). The small fraction of time gill-nets and trawls actively sample can limit the robustness of identifying spatiotemporal distribution patterns. This is of particular concern for species with patchy distribution and transient fishes with large activity spaces and movement patterns (Gregalis 2009, Reese Robillard et al. 2010).

Not surprisingly, the gear costs associated with telemetry research are significantly greater than traditional gears commonly used, potentially discouraging groups from implementing telemetry studies. Telemetry gear can clearly be a financial burden with initial purchases; however, the magnitude of these costs are reduced with continued use of equipment,

particularly the hydrophones, in subsequent research. For example, the cost of replicating the experiments from the two telemetry case studies presented would be approximately 50% (fine-scale habitat-use case study) and 30% (estuarine-scale seasonal distribution case study) of the original cost. Moreover, collaborative networks such as Ocean Tracking Network (OTN), Atlantic Cooperative Telemetry (ACT), and Florida Atlantic Coast Telemetry offer expanded spatial coverage through networking telemetry users, although at a much coarser spatial resolution based on the arrangement of hydrophones within versus among participating research projects. The Pacific Ocean Salmon Tracking (POST) project presents a valuable template highlighting a collaborative initiative that maximized the return on investments by establishing a shared network of hydrophones used in a way that benefited the research of multiple state, federal, and academic agencies within a single estuarine system (Welch et al. 2003).

Although in this review we have expressed support for using telemetry to resolve questions regarding spatial ecology of fish, we have also highlighted the limited capacity in using this gear alone to address some of the identified research topics directly (i.e. community and population dynamics). Combining the use of telemetry with alternative tools and sampling gears can allow researchers to address a broader scope of research (Friedl et al. 2013, Matich and Heithaus 2014, Lowerre-Barbieri et al. 2016, Freedman et al. 2015, Mahoney et al. 2018), but less than half of the telemetry studies identified in this review incorporated additional sampling tools and gears in their study design. Combining telemetry sampling with other gears and sampling tools (i.e. stable isotopes, diet analysis, and fisheries independent surveys), gives researchers a greater ability to explain ecological processes rather than simply serving as an observational platform.

The results from the two case studies highlight how the advantages and limitations of sampling designs previously identified in this review can influence our understanding of outcomes from estuarine research. First, use of traditional gears to sample individual habitats in constrained spatial locations can significantly limit spatiotemporal resolution of habitat selectivity. This was highlighted in the lack of significant red drum catches in the gill nets in the fine-scale habitat selectivity case study. Improvements can be made to sampling designs (i.e. increased soak time) although this is unlikely to provide the resolution necessary to accurately identify fine-scale habitat selectivity (Rotherham et al. 2006). This is of particular concern for initiatives encouraging standardization of sampling designs for monitoring estuarine habitats (sensu Baggett et al. 2015). Although costs are high, we encourage future research of habitat selectivity at similar spatial scales to incorporate telemetry into sampling designs to gain enough spatiotemporal resolution of fish behavior. However, in the estuarine-scale seasonal distribution case study, the long-term gill-net survey resulted in comparable spatiotemporal distribution patterns as telemetry monitoring. We believe this reflects the limited spatiotemporal resolution requirements for assessing distribution at the scales monitored (daily presence/absence at the estuarine scale) in these studies. Although twice monthly gill-net sampling was sufficient in identifying seasonal distribution, detailed understanding of the causes of observed patterns requires knowledge of movement parameters and behavior, which can be obtained using telemetry.

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TABLES

Table 3.1 List of publications identified in the Web of Science literature search and extracted sampling metrics. Acoustic telemetry citations marked with an asterisk denote studies that used active tracking approaches. Data entries identified with N/A indicate the target information was not sufficiently provided in the publication text.

Gear	Citation	Research Topic	Species Count	Fish Count	Average Fish Size (mm)	Area Monitored (km ²)	Study Duration (days)	Monitoring Effort
<i>Telemetry</i>	*Alr et al. 2015	Fine Scale Habitat Selectivity	1	20	242.0	N/A	700	0.0571
	Callihan and Cowan 2013	Residency	1	172	512.5	7.54	949	0.9589
	Clark et al. 2016	Survival, Movement Parameters	1	1,859	126.3	14.87	1062	1.0000
	Dance and Rooker 2015	Fine Scale Habitat Selectivity	2	22	304.0	0.01	285	0.1053
	Dance and Rooker 2015	Broad Scale Habitat Selectivity, Response to Abiotic	2	22	304.0	6.50	285	0.2702
	*Farris et al. 2016	Fine Scale Habitat Selectivity	1	20	242.0	N/A	700	0.0571
	Farris et al. 2016	Habitat Selectivity, Movement Parameters ,Connectivity	1	99	252.0	3.39	308	1.0000
	Freedman et al. 2015	Connectivity	5	80	560.0	0.38	738	0.9892
	*Freedman et al. 2016	Habitat Selectivity	1	20	435.0	N/A	280	0.1275
	Gahagan et al. 2015	Population Contigents	1	51	664.0	150.10	912	0.6009
	Goetz et al. 2015	Survival, Movement Parameters	1	337	188.0	24.64	N/A	N/A
	Healy et al. 2017	Survival, Movement Parameters	1	243	200.0	19.71	205	1.0000
	Ajemian et al. 2018	Habitat Selectivity, Response to Abiotic Conditions, Residency	1	36	45.8	10.63	723	1.0000
	Lowerre-Barbieri et al. 2014	Spawning Activity, Residency	1	31	643.0	0.95	540	0.5000
	Lowerre-Barbieri et al. 2013	Habitat Selectivity, Spawning Activity	1	32	300.0	0.41	200	1.0000
	*Lowerre-Barbieri et al. 2016	Spawning Activity, Residency	1	20	765.0	N/A	1251	0.0022
	Lowerre-Barbieri et al. 2016	Spawning Activity	1	20	765.0	1.32	1251	0.3805
	Melnychuk et al. 2014	Survival, Movement Parameters	1	398	181.0	56.04	N/A	N/A
	Moore and Berejikian 2017	Survival, Movement Parameters	1	203	193.0	11.71	160	1.0000
	*Friedl et al. 2013	Survival	1	123	165.0	N/A	250	0.0064
	Friedl et al. 2013	Survival	1	123	165.0	7.07	250	1.0000
	Wegener et al. 2017	Habitat Selectivity	1	22	920.0	1.14	1825	1.0000
	Fox et al. 2018	Juvenile Habitat Selectivity	1	9	371.0	3.52	730	1.0000
	Stehlik et al. 2017	Response to Abiotic Conditions	3	168	550.0	22.67	400	0.8425
	Fodrie et al. 2015	Individuality	1	34	550.0	0.09	227	0.7048
	Kenworthy et al. 2018	Connectivity	1	34	550.0	9.62	227	0.7048
	Mahoney et al. 2018	Edge Effects	1	8	471.0	0.09	227	0.2070
<i>Gill-net</i>	Matich et al. 2017	Habitat Selectivity	2	10,753	1290.0	37.59	14235	0.1647
	Sulak et al. 2014	Survival, Growth	1	1,192	1051.0	0.03	6935	N/A
	Ellis et al. 2018	Survival	1	3,221	436.0	12.90	2920	0.1260
	Peer and Miller 2014	Response to Abiotic Conditions	1	N/A	800.0	0.25	8760	0.0020
	Schrandt et al. 2016	Habitat Selectivity	2	574	372.0	0.26	730	0.0080
	Schrandt et al. 2015	Habitat Selectivity, Population Dynamics	1	N/A	403.0	8.57	4015	0.0119
	Bahr et al. 2017	Population Dynamics	1	610	737.0	0.70	1095	0.0055
	Brown et al. 2014	Habitat Selectivity, Community Dynamics	24	217	N/A	0.00	122	0.0548
	Friedl et al. 2013	Community Dynamics	7	477	375.0	0.30	730	N/A
	Froeschke and Froeschke	Habitat Selectivity	1	N/A	N/A	45.30	12775	0.1491
	Jones and Able 2015	Habitat Selectivity	15	5,519	322.0	0.01	730	0.0134
	Pierson and Eggleston 2014	Community Dynamics	51	3,031	N/A	0.01	1095	0.0067
	Stehlik et al. 2017	Response to Abiotic Conditions	3	1,285	2611.0	0.10	730	0.0027
	Fox et al. 2018	Juvenile Habitat Selectivity	1	1	920.0	0.14	730	0.0011
	Ziegler et al. 2017	Habitat Selectivity, Community Dynamics	22	186	N/A	0.002	152	0.1315
	Bangley et al. 2018	Range Expansion	1	70	812.0	19.62	5110	0.1461

Table 3.1. Cont'd

<i>Trawl</i>	Brown et al. 2014	Habitat Selectivity, Community Dynamics	19	1,055	N/A	0.01	122	0.0009
	Friedl et al. 2013	Community Dynamics	3	N/A	N/A	0.12	730	0.0003
	Buchheister et al. 2013	Response to Abiotic Conditions, Community Dynamics	98	272,083	300.0	93.05	3650	0.0138
	Essington et al. 2013	Population Dynamics	14	N/A	203.0	0.52	7300	0.0002
	Gut and Curran 2017	Response to Abiotic Conditions, Community Dynamics	42	2,448	35.3	0.01	730	0.0001
	Baillie et al. 2015	Community Dynamics	71	139,663	N/A	0.82	730	0.0006
	Flaherty-Wailia et al. 2015	Recruitment, Habitat Selectivity	1	823	150.0	2.47	1460	0.0052
	Switzer et al. 2015	Recruitment, Habitat Selectivity	1	617	180.0	2.98	1825	0.0076
	Valenti et al. 2017	Community Dynamics	69	29,511	N/A	NA	1095	0.0018
	Gorecki and Davis 2013	Response to Abiotic Conditions, Community Dynamics	114	188,576	80.0	0.48	1034	0.0014
	Hammock et al. 2017	Foraging Dynamics	1	1,318	N/A	NA	1095	0.0241
	Lazzari 2013	Habitat Selectivity	4	3,395	64.0	0.82	2190	0.0021
	O'Connell et al. 2014	Community Dynamics	N/A	N/A	N/A	4.65	3650	0.0016

Table 3.2 List of research topics identified in the selected publications for each gear type. Values represent the proportion of papers within each gear category that examined the respective research topic.

Research Topic	Telemetry (n=28)	Gill-net (n=16)	Trawl (n=13)
Habitat Selectivity	0.36	0.50	0.31
Population Dynamics	0.25	0.19	
Community Dynamics		0.25	0.62
Movement Parameters	0.36		
Connectivity	0.14		
Spawning Behavior	0.11		
Response to Abiotic Conditions	0.11	0.13	0.23
Spatiotemporal Abundance		0.13	0.08
Population Contingents	0.04		
Foraging Dynamics			0.08
Individuality	0.04		
Edge Effects	0.04		
Range Expansion		0.06	

Table 3.3 Sampling metrics quantified for each gear type examined. Values represent mean $\pm$ SE with ranges listed below in parentheses.

Gear	Species Count	Fish Count	Average Fish Size (mm)	Coverage Area (km²)	Study Duration (days)	Monitoring Effort
Telemetry	1.3 $\pm$ 0.2 (1 - 5)	156 $\pm$ 68 (8 - 1,859)	395 $\pm$ 44 (46 - 920)	16.0 $\pm$ 6.9 (0.01 - 150.10)	587 $\pm$ 86 (160 - 1,825)	0.62 $\pm$ 0.08 (0.002 - 1)
Gill-Net	8.4 $\pm$ 3.4 (1 - 51)	2,087 $\pm$ 851 (1 - 10,753)	844 $\pm$ 184 (322 - 2,611)	7.9 $\pm$ 3.6 (0.002 - 45.30)	3804 $\pm$ 1,146 (122 - 14,235)	0.06 $\pm$ 0.02 (0.001 - 0.165)
Trawl	36.4 $\pm$ 12.0 (1 - 114)	63,948 $\pm$ 31,463 (617 - 272,083)	145 $\pm$ 35 (35 - 300)	9.6 $\pm$ 8.4 (0.01 - 93.05)	1,970 $\pm$ 536 (122 - 7,300)	0.005 $\pm$ 0.002 (0.0001 - 0.0240)

Table 3.4 List of supplies and cost associated with sampling gear required for the gill-net and telemetry surveys associated with the two case studies examined.

Gear	Supplies	Case Study 1		Case Study 2	
		Quantity	Cost	Quantity	Cost
Gill-net					
	Gill-nets	12 @ 10 meters	\$ 498.00	2 @ 240 meters	\$ 1,637.00
	Marker Floats	24	\$ 162.00	18	\$ 121.50
	Replacement Netting	4 (sold by lb.)	\$ 71.80	32 (sold by lb.)	\$ 574.40
	Total Cost		\$ 731.80		\$ 2,332.90
Acoustic Telemetry					
	Hydrophones	8	\$ 11,840.00	45	\$ 66,600.00
	Transmitters	34	\$ 11,220.00	91	\$ 30,030.00
	Reference tags	2	\$ 660.00	0	\$ 0.00
	Moorings	8	\$ 240.00	45	\$ 1,350.00
	Data analysis	1	\$ 2,400.00	0	\$ 0.00
	Replacement Hydrophones	1	\$ 1,480.00	5	\$ 7,400.00
	Replacement Moorings	1	\$ 30.00	5	\$ 150.00
	Total Cost		\$ 27,870.00		\$ 105,530.00

FIGURES

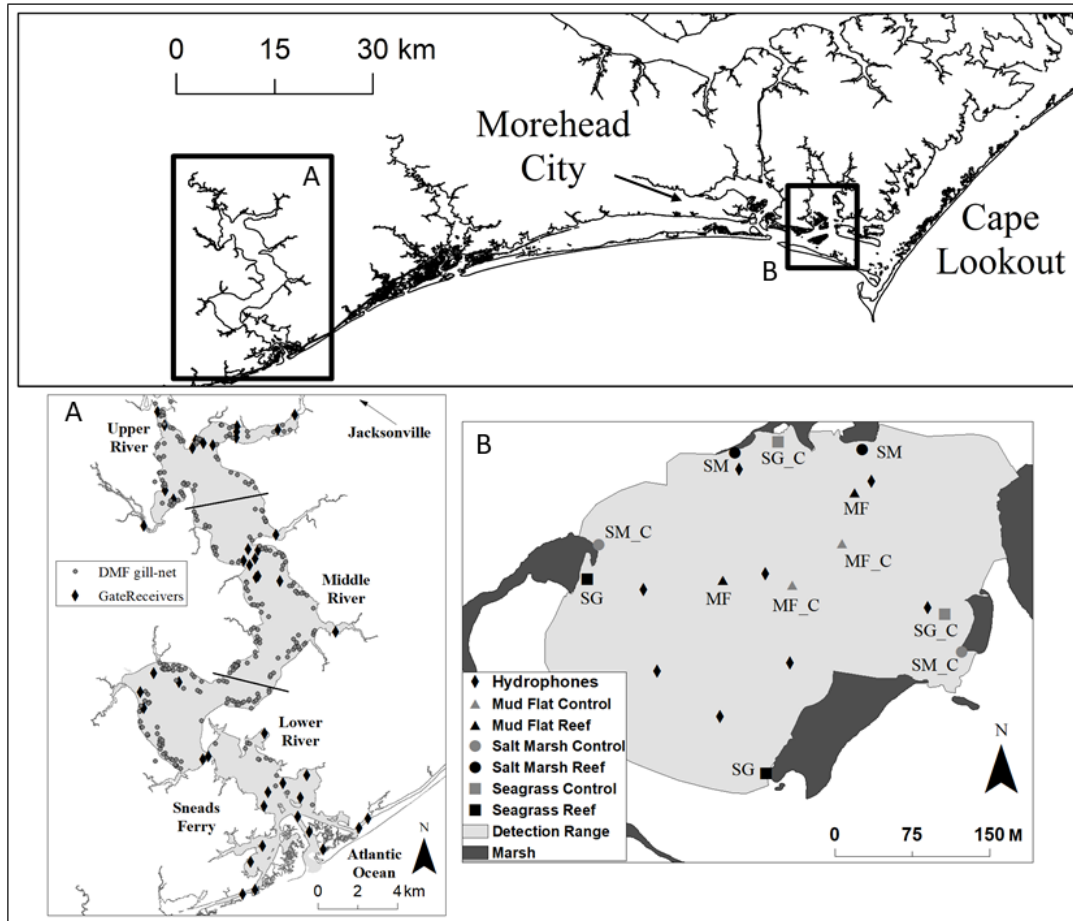


Figure 3.1 Map of the sampling locations for A) NRE case study examining seasonal distribution of black drum and red drum and B) Middle Marsh case study examining the fine-scale selectivity of restored oyster reefs. Cross sectional lines in the NRE map indicate river section delineation used in analysis.

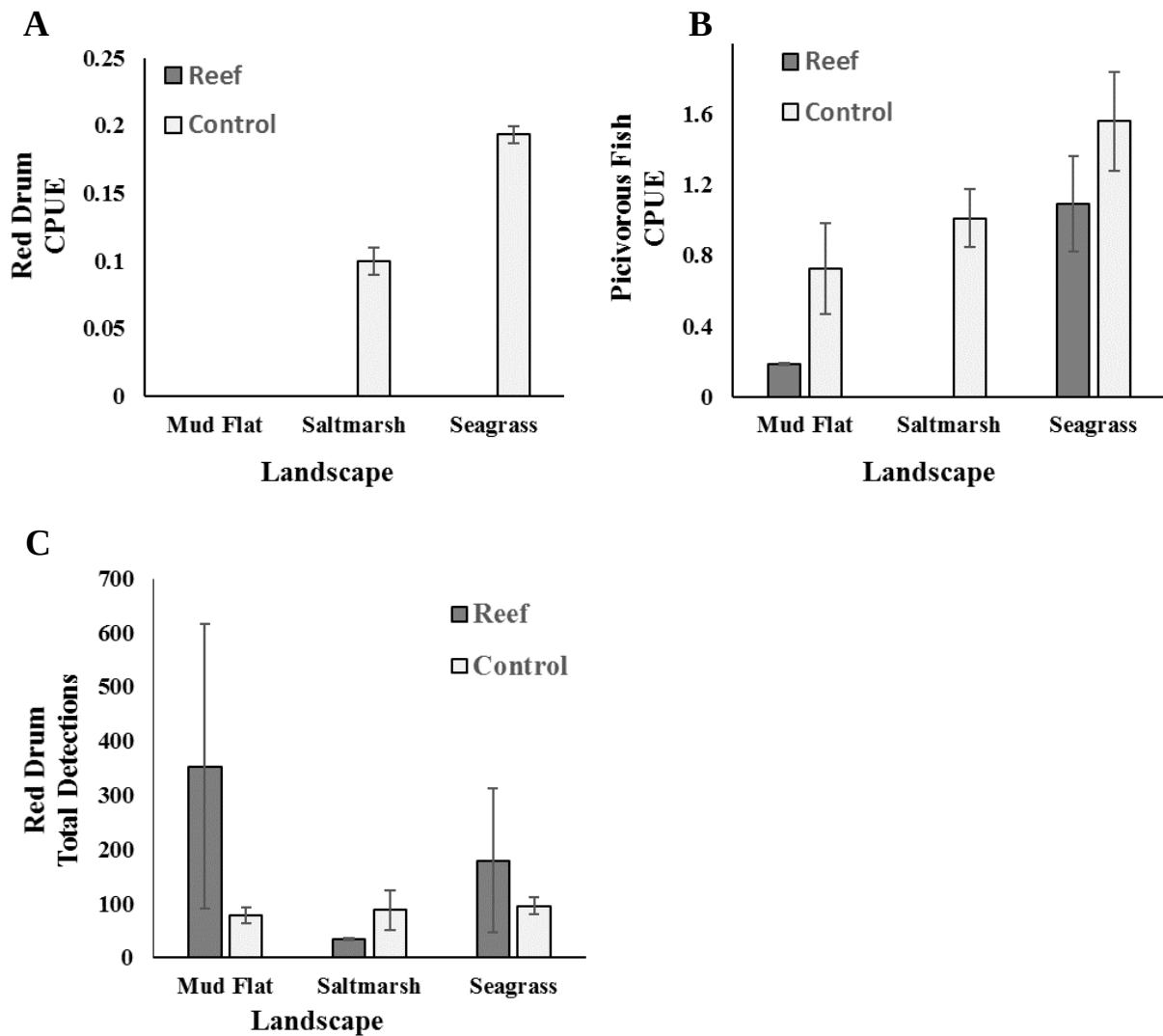


Figure 3.2 Patterns of fine-scale habitat selectivity in fine-scale habitat selectivity case study. Bar graphs show catch rate patterns for A) red drum and B) piscivorous fishes and C) total telemetry detections for red drum at restored oyster reefs and control sites within the three landscapes monitored. CPUE values for both red drum and piscivorous fish represent delta densities. All values are mean $\pm$ SE.

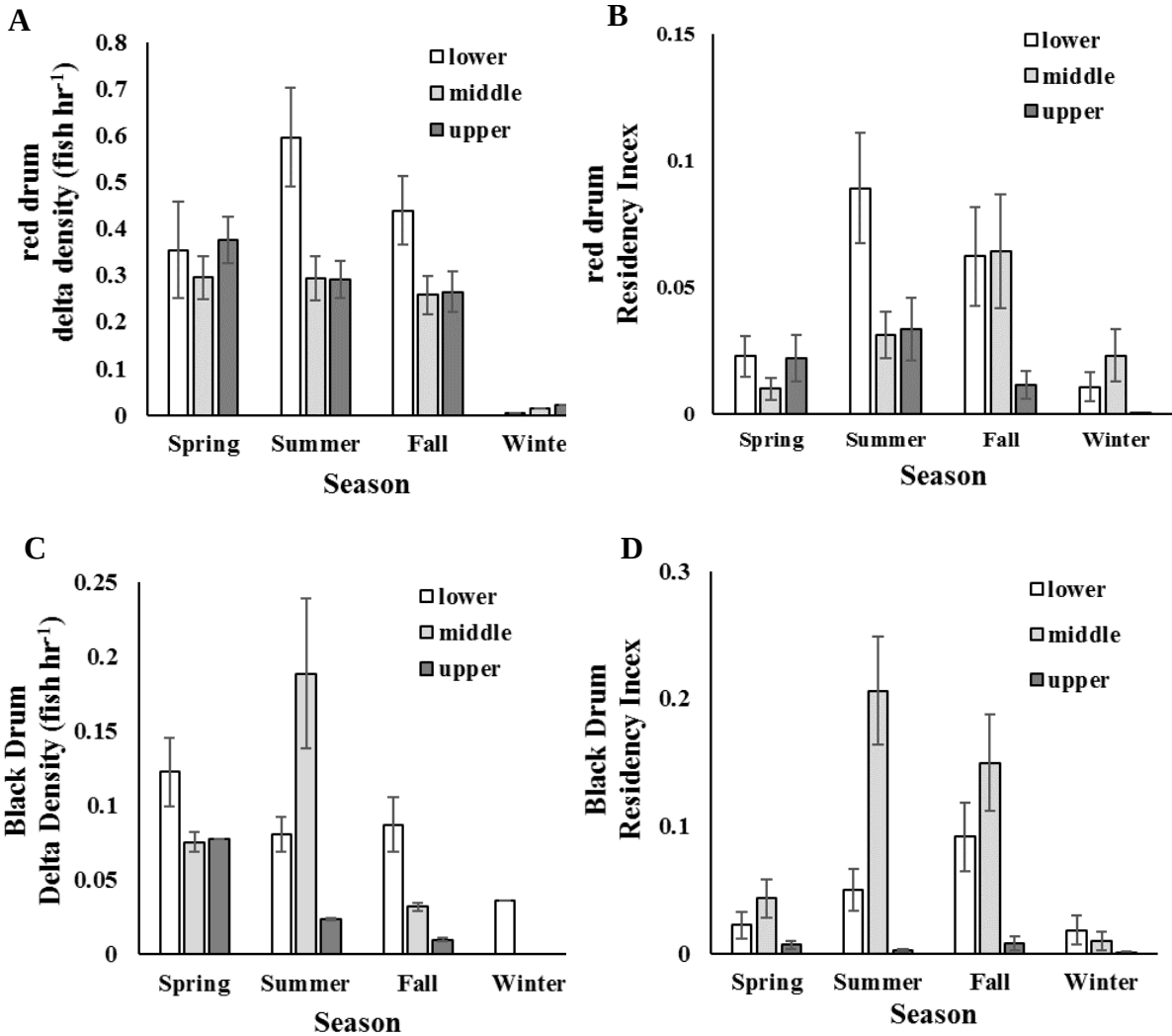


Figure 3.3 Seasonal distribution patterns of red drum (A-B) and black drum (C-D) in the DMF long-term gill-net (delta density) and telemetry (residency index) surveys respectively. All values are mean $\pm$ SE.

CHAPTER 4: RESTORATION GOALS, SPATIAL-SCALE, AND SPECIES IDENTITY INFLUENCE HOW CULTCH SHELL ENHANCEMENT AND ARTIFICIAL REEFS PROVIDE HABITAT SUBSIDIES FOR ESTUARINE FISHES

Introduction

Anticipated linkages between the availability of healthy coastal habitats and production of commercially and recreationally important fisheries has been one important driver of ecosystem conservation efforts (Turner 1977, Blaber 2009, Nagelkerken et al. 2015). With declining coastal biogenic habitats worldwide, stakeholders have dedicated significant resources and effort to protect and restore critical habitat. Habitat restoration, routinely applied to recover/increase the abundance of coastal marine habitats, has been conducted in a variety of contexts (e.g. coral transplanting, planting aquatic vegetation, deployment of substrate to promote bivalve settlement, etc.) (Powers and Boyer 2014). While these efforts are unified under a clear objective of preserving essential habitat, successfully restoring habitats in a manner that optimizes ecological functions and services remains challenging in most environments. With limited resources available for habitat conservation, it is critical that stakeholders fully understand the biological responses associated with restoration to determine whether desired outcomes and goals of projects are achieved and to effectively design future initiatives.

Oyster reefs established by the eastern oyster, *Crassostrea virginica*, have been highly targeted in habitat conservation over the last several decades in response to: (1) global-scale loss of oyster biomass (Beck et al. 2011, Zu Ermgassen et al. 2012, La Peyre et al. 2014), and (2) research highlighting the value of ecosystem services associated with oyster reefs (Lehnert and

Allen 2002, Grabowski et al. 2012). Over the last century, construction of man-made artificial structures in estuarine systems has been employed to facilitate the development of new oyster reefs to offset negative impacts of population declines. Generally constructed by building mounds using a variety of materials (e.g. concrete rubble, relic shell, and concrete fish domes), artificial reefs are commonly deployed in areas void of structured habitat (Theuerkauf et al. 2015). Following provision of hard settlement substrate, natural processes of settlement, growth, and mortality determine the trajectory of constructed (“restored”) reefs. Indeed, careful siting and tactical deployment of hard substrates within estuarine systems has proven successful for developing new sustainable oyster reef habitat (e.g., Fodrie et al. 2014; Ziegler et al. 2018)

Unlike other estuarine biogenic habitats (i.e. seagrass, saltmarsh, and mangroves), oysters are also harvested for consumption in a multi-million-dollar industry. Therefore, stakeholders have regularly invested in programs to enhance oyster habitat specifically designated for eventual shellfish harvest at those sites (i.e., habitat degradation). Although both ecosystem-service-orientated restoration and harvest-focused enhancement utilize similar methods of creating hard substrates suitable for oyster settlement, survival, and growth, enhancement differs from restoration in the intended long-term goals and objectives. Success of an enhancement reef (open to harvest) is ultimately dependent on the amount of marketable oyster biomass harvested from the created habitat while restoration (closed to harvest) strives to restore and sustain long-term ecosystem services and functions (Coen and Luckenbach 2000).

Oyster reef habitat forms complex three-dimensional structures which have regularly been shown to support more diverse faunal communities compared to unstructured habitats (Tolley and Volety 2005, Coen et al. 2007, Zu Ermgassen et al. 2016). Addition of new habitat subsidies associated with oyster reef restoration can also increase productivity of economically

prized fishes (Grabowski et al. 2012, Humphries and La Peyre 2015, Keller et al. 2017). These examples, however, are derived from restored reefs built with harvest restrictions. The process of removing oysters on enhancement reefs alters the overall structure of the habitat, potentially degrading long-term sustainability of the reef and the ecosystem services it provides (e.g. provision of habitat for fish) (Lenihan and Micheli 2000). Stakeholders commonly assume and advertise that the addition of habitat associated with oyster reef enhancement projects is beneficial to fish; however, research exploring how fish identify and utilize subtidal enhancement reefs established for the put-and-take fishery is not well supported by targeted experimental assessments.

Quantifying the spatiotemporal dynamics of how fish utilize various types of man-made oyster reef habitat is critical for estimating the delivery of ecosystem services provided by these habitats. We utilized an acoustic tagging/tracking approach to continuously monitor patterns of habitat selection (i.e., restored reefs, shellfish enhancement sites, and unstructured reference sites) for sub-adult red drum (*Sciaenops ocellatus*), sub-adult black drum (*Pogonia cromis*), and southern flounder (*Paralichthys lethostigma*), three mobile, highly prized fishes in North Carolina estuaries. Additionally we explored the relationships between habitat selection and relative metrics of habitat quality of enhancement sites which could be altered due to the process of harvesting oysters. We asked three primary questions regarding habitat choice of these fishes: 1) Do fish spend more time at man-made oyster reef habitat (i.e., restored reefs or shellfish enhancement sites) compared to unaltered reference sites? (2) Does fish utilization of shellfish enhancement sites scale with density of reef-associated invertebrates (i.e., prey availability) and overall structural complexity (i.e., oyster abundance)? and (3) Does fish utilization of a site scale

with spatial magnitude of the enhancement effort (i.e., amount of material deposited on the seabed at cultch enhancement sites)?

Methods

Study Area

Our study was conducted in the New River Estuary (NRE), North Carolina (NC). The broad, shallow, periodically stratified NRE covers an area of approximately 88 km², draining a watershed of 462 km² and connected to the ocean by the New River Inlet (Fig. 4.1). Surrounded mostly by Marine Corps Base Camp Lejeune, large portions of shoreline in the NRE are relatively unaltered and free of development. Salinity gradients in the NRE range between ~0-10 ppt near Jacksonville, NC, to 35 ppt at the Inlet. Along the main axis of the NRE, depths reach 4-6 m and the bottom substrate is muddy. Along the margins of the NRE (200-400 m from shore) the depths are typically 1-3m and the bottom substrate is sandy mud. Tide ranges in the NRE are generally <0.3 m (Ensign et al. 2004).

Multiple programs operated by the NC Division of Marine Fisheries (DMF) have contributed a variety of man-made reef habitat in North Carolina estuaries. The shellfish enhancement program has deployed approximately 500,000 bushels of cultch material (fossil shell material and marl) annually to create more than 2000 oyster (cultch) reef habitat enhancement sites within NC estuaries. The quantity of cultch material used to create enhancement site ranges between 457 and 70,516 bushels per site. Oysters can be harvested at these sites as soon as they reach legal size (i.e., 3", or approximately 2 years post deployment of cultch substrate). Additionally, the NC DMF artificial reef program, in cooperation with nongovernment organizations and municipalities, has committed to restoring oyster populations

and enhancing estuarine and offshore habitat for fishes using artificial structures. NC DMF maintains twenty-two estuarine artificial reef sites ranging in size from five acres to over 150 acres. Each site consists of a mosaic of reefs constructed using materials of opportunity (e.g., pipes, castings, rubble, marl, and reef balls) and ranging in size and complexity from single reef balls to moderately sized (~3-5m diameter) mounds rising 1-2m off the substrate. Artificial reef habitats are open to fishing for finfish; however, they are closed to shellfish harvest.

Since 2003, the NC DMF has constructed over 50 cultch enhancement reefs in the lower NRE (Fig. 4.1). In some locations, cultch reefs were created within proximity (100-200 meters) to each other during separate years forming a cluster of sites varying in age. We selected six cultch sites/clusters, paired with six non-enhanced reference sites, to monitor the habitat use of focal fish species. Specifically, the cultch sites we monitored contained between two and six individual cultch reefs within listening distance of an acoustic hydrophone (see tagging and tracking section for more detail on hydrophone specifications). We selected six sites to capture a range of reef sizes (cumulative quantity of cultch material deployed at that site) and locations throughout the lower NRE (Table 4.1) (Fig. 4.1). The spatial footprint of the selected cultch reefs range between 0.15 and 10.02 acres. Although various materials have been used in constructing cultch reefs (e.g., oyster shell, clam shell, and marl), we selected sites consisting of oyster shell only. Non-enhanced reference sites were selected to represent similar abiotic characteristics as the paired cultch site (i.e., similar depth, water temperature, salinity, and geographical features).

In addition to the six paired enhancement/reference sites, we also explored how fish utilized an artificial reef habitat constructed by NC DMF in the NRE. The 21.85-acre estuarine artificial reef complex (AR-398), located in the central NRE, contains hundreds of mounds built using concrete rubble material. Each mound consists of approximately 1.86 cubic yards of

material in a spherical cone (~ 1-m high), creating a field of high relief structure over what was previously relatively flat, unstructured bottom. Like the cultch reefs, we identified a paired reference site to explore habitat use by fishes which closely represented the environmental characteristics of AR-398 (Fig. 4.1).

Study Species

We monitored habitat use of sub-adult red drum (*Sciaenops ocellatus*), sub-adult black drum (*Pogonia cromis*), and southern flounder (*Paralichthys lethostigma*) in the NRE. These species are valued in both recreational and commercial fisheries throughout the southeast Atlantic and Gulf of Mexico. All three species have been documented utilizing subtidal oyster reef habitats for refuge and foraging in estuarine systems (Lehnert and Allen 2002, Brown et al. 2008, Robillard et al. 2010, Plunket and Peyre 2005). Therefore, a working hypothesis is that oyster reef habitat subsidies will support higher fitness and ecosystem carrying capacity for these large estuarine fishes. These species are also highly mobile, highlighting the need to understand the spatiotemporal patterns with which they occupy habitats across complex estuarine landscapes to rigorously quantify the functional role of natural and human-constructed habitats for finfish production.

Tagging and tracking

To detect the frequency and duration of site/habitat visits by individually tagged fish, we deployed a single Vemco VR2W hydrophone at each of the six cultch reef sites and six paired cultch reference sites. At the cultch reef sites, we placed the hydrophone in a central location relative to the footprint of all cultch material at that site. Reference sites were targeted to maintain a minimum distance of 750 meters (1.5X the max detection range of 500 meters observed for all transmitters used in this study) between hydrophones to eliminate the possibility

of simultaneous detections at enhancement and reference sites. The total coverage area of each hydrophone (~190 acres) is much greater than the spatial extent of the cultch sites (max = 10.02 acres). Reference sites were located greater than 500 m from any cultch reefs or shellfish leases in the NRE. We monitored the frequency and duration of site/habitat visits by fishes at the artificial reef complex using a similar approach. We deployed two hydrophones at AR-398 to address concerns of reduced detection probability resulting from the amount of vertical relief of the rubble mounds. To compare the presence/absence of tagged fishes at the artificial reef complex with a non-restored habitat, we deployed one hydrophone at a similar estuarine environment, but without any hard substrate, ~ 1.25 km southeast of AR-398.

We acoustically tagged and released 55 sub-adult red drum (529 ± 12 mm total length [TL]), 36 sub-adult black drum (455 ± 05 mm TL), and 292 southern flounder (390 ± 2 mm TL) from a variety of locations throughout the full extent of the NRE. Red drum and black drum tagging occurred between August 2012 and October 2014. Tagging of southern flounder occurred between August 2012 and November 2015. Data collection commenced when the first fish were tagged and continued through the end of December 2015. A coded acoustic transmitter was implanted into the body cavity of fishes following procedures outlined in Dresser and Kneib (2007). All transmitter insertion surgeries were conducted from a small research vessel held at the fish's capture location, and fishes were returned to the water after a ~30 min recovery and observation period. Red drum and black drum were tagged with V13 VEMCO transmitters (nominal delay of 120 sec. with an estimated 1117 days of battery life) while V9 VEMCO transmitters (nominal delay of 90 sec. with an estimated 350 days of battery life) were used for southern flounder. Each transmitter emitted a unique pulsed chirp, which was used to identify the presence of individual fish within range of a hydrophone, including a time stamp for each

detection (detection data downloaded every three months). Due to potential discrepancies in behavior resulting from capture, tagging, and subsequent release back into the environment, we excluded detection data from the first 24 hours after being released. Prior to analysis, detection data were filtered for false detections using VEMCO's data processing software (VUE).

Additionally, we ensured that all detections were from live individuals. A deceased individual could be identified when a transmitter was detected continuously at a single hydrophone, with no detections occurring at any other stations, throughout the duration of the study or tag life. Range testing conducted prior to the start of the study identified a maximum detection range ~ 500m. Detection distance was highly influenced by water depth, current velocity, and wind conditions (unpublished personal observations).

Habitat Sampling

We quantified densities of live oysters (ecosystem structure) and macrofauna (potential prey fields) at each cultch reef and non-enhanced reference site during April 2013. At each site we collected five 10-cm diameter cores. One core was taken at the center of the sampling area (center of a cultch reef or near the hydrophone at the non-enhanced references sites) with an additional four cores taken haphazardly along four separate 50-m transects moving away from this initial location (five cores per site). All individuals were identified at the lowest taxonomical level possible. Additionally, at the six cultch reef sites we quantified densities of live oysters and mud crabs from ten 0.25m² quadrats where all exposed shell material and associated fauna were excavated. All samples from the cores and quadrats were processed immediately after being lifted aboard the research vessel. Finally, we obtained information on the number of bushels of cultch shell deployed at each enhancement site from the NC DMF website (<http://portal.ncdenr.org/web/mf/cultch-planting-maps-data>).

Analyses

To compare habitat use of fishes between reefs (cultch and AR-398) and the paired reference sites, we quantified the number of detections·day⁻¹ and the number of visits at each site as two separate metrics of habitat choice (sense Fodrie et al. 2015). Because of occasional absences of hydrophones during the study (e.g., removal preceding storm landfall, routine maintenance, and equipment failure), analysis of habitat choice was restricted to days when a hydrophone was present at both paired sites (reef and reference). Distinct visits at a site were defined when a series of detections for an individual fish was recorded followed by a period of at least 30 minutes during which the fish was not detected at the site. To include an event in our metrics of habitat use (total detections and distinct site visits) individuals must have been detected a minimum of five times (red drum or black drum) and seven times (southern flounder) during a distinct visit. This helped eliminate detections due simply to fishes transiting by/past our sites along movement corridors. These species-specific detection minimums also reflected the different chirp frequencies of the transmitters, as well as mobility patterns of species, considered in this study.

To assess whether fishes were detected more at the cultch reef sites or the non-enhanced reference sites, we first quantified the number of detections·day⁻¹ at each site (i.e., hydrophone) for each species separately as well as a total for all three species combined. For each species, as well as all species combined, we used a two-tailed Wilcoxon signed-rank test to compare the mean detections·day⁻¹ between paired cultch reef and non-enhanced reference sites (N = 6, where site was independent unit of replication). Analysis of detection data at AR-398 was treated differently to account for the additional hydrophone at the artificial reef complex and the limitation of only having a single pairing of sites for comparison. First, due to the proximity of

the two hydrophones at AR-398, transmissions from individual tags were often simultaneously detected. When this occurred, one of the detection records was removed to ensure that a single transmission was not double counted. Next, because detectability at AR398 was doubled (i.e. two hydrophones), we used the mean number of detections recorded each day from these two hydrophones to represent the daily number of detections at the artificial reef. Lastly, because we were limited to only one artificial reef site we quantified the number of detections·fish⁻¹·day⁻¹ with each day treated as a replicate in our analysis (N = 1211 replicate days). Daily number of detections·fish⁻¹ at AR-398 and the non-restored reference were compared using a two-tailed Wilcoxon signed-rank test.

Next, we quantified the number of times fish visited each cultch reef and non-enhanced reference site. The total number of visits between paired cultch reef and non-enhanced reference sites (N = 6 replicate sites) were compared using a two-tailed Wilcoxon signed-rank test. Visitation data at the artificial reef complex, similar to total detections, was treated differently due to limitations of monitoring only a single pairing of artificial reef and reference sites. For fish detected at AR-398 or the paired non-restored reference site, we quantified the number of visits·fish⁻¹ at each location. We used a two-tailed Wilcoxon signed-rank test to compare the number of visits·fish⁻¹ between the artificial reef and the reference sites. The Wilcoxon signed-rank test was utilized for our analyses due to violations of normality in the detection and visitation data. We considered *p* values (without denoting an arbitrary alpha), effect sizes, and variances to evaluate the strength of evidence for preference or avoidance of man-made habitats (cultch reefs and AR-398) versus reference habitats (Hurlbert et al. 2009, Murtague 2014, Lopez-Duarte et al. 2016). All statistical analyses were conducted in JMP Pro 12.

Finally, using regression analysis, we explored the relationships between fish habitat use (detections·day⁻¹) and densities of live oysters (individuals·m⁻²), select macrofauna (individuals·m⁻²), as well as quantity of cultch material deployed (# bushels), across enhancement cultch reefs and non-enhanced reference sites. Our analysis of macrofauna densities focused on live oysters, non-oyster bivalves (hard clam *Mercenaria Mercenaria*, razor clam *Ensis directus*, jingle shell *Anomia simplex*, dwarf surf clam *Mulinia lateralis*), and mud crabs. Regression analysis was conducted in R.

Results

We recorded 256,978 detections to examine the habitat use of the shellfish enhancement reef (i.e., cultch) sites, AR-398, and the paired reference sites across all three species in the NRE. Red drum (191 ± 24 days at liberty fish⁻¹), on average, were detected for the longest duration compared to black drum (147 ± 17 days at liberty fish⁻¹) and southern flounder (86 ± 5 days at liberty fish⁻¹). Overall, we detected 36 (65%) red drum, 27 (75%) black drum, and 111 (38%) southern flounder at one or more of our monitoring locations. Detections at the enhancement reefs and enhancement reference sites were greatest for southern flounder (94,432 detections from 85 individuals) followed by black drum (47,750 detections from 22 individuals) and red drum (21,255 detections from 33 individuals). Conversely, at AR-398 and the AR-398 reference site, black drum (88,162 detections from 23 individuals) detections far outpaced both southern flounder (5,079 detections from 43 individuals) and red drum (300 detections from 11 individuals).

Mean daily detections and visit frequency across all three species were approximately 4.3 x and 3.5 x greater respectively at the enhancement reference sites relative to the enhancement

reef sites. This trend was more statistically clear for mean daily detections ($Z = -10.5$, $P = 0.031$) (Fig. 4.2) than for mean number of visits ($Z = -7.5$, $P = 0.156$) (Fig. 4.3). These trends were highly influenced by black drum which on average recorded 9.3 x and 4.7 x more detections ($Z = -9.5$, $P = 0.063$) and number of visits ($Z = -10.5$, $P = 0.031$) respectively at the enhancement reference sites compared to the enhancement reef sites (Fig. 4.4). Mean daily detections and mean number of visits for southern flounder also trended greater at the enhancement reference sites compared to the enhancement reef sites, although statistical support for these being reliable differences were weak (daily detections: $Z = -6.5$, $P = 0.218$; number of visits: $Z = -7.5$, $P = 0.156$) (Figs. 4.2, 4.3). No statistically distinguishable differences were observed in daily detections or visit frequency between the two site types for red drum (daily detections: $Z = -4.5$, $P = 0.438$; visits: $Z = -4.5$, $P = 0.438$) (Figs. 4.2, 4.3) although on average, the number of visits at enhancement reference sites were approximately 1.7x greater than visits at enhancement reef sites.

Unlike enhancement reefs, mean daily detections ($Z = 122,771.5$, $P < 0.001$) and visit frequency ($Z = 664.5$, $P < 0.001$) across all species was significantly greater at AR-398 compared to the AR-398 reference site (Figs. 4.4, 4.5). These patterns, however, were driven primarily by black drum daily detections and visit frequency which on average were 64.5 x ($Z = 136,171.5$, $P < 0.001$) and 28.5 x ($Z = 125$, $P < 0.001$) greater respectively at AR-398 relative to the AR-398 reference site (Figs. 4.4, 4.5). Although mean daily detections per fish for red drum and southern flounder trended higher at the AR-398 reference site compared to AR-398, these trends were driven by a few exceptional days and reliable patterns were otherwise statistically indistinguishable for both species (RD: $Z = -2,425.5$, $P = 0.389$; SF: $Z = 2,149$, $P = 0.671$) (Fig. 4.4). No statistically distinguishable differences were identified in visits between AR-398 and the

AR-398 reference for either red drum ($Z = 7.5$; $P = 0.534$) or southern flounder ($Z = 36.5$; $P = 0.658$), and mean visits between sites were similar for both red drum and southern flounder.

We observed no statistically distinguishable relationships between mean daily detections of each fish species individually or all species combined and densities of live oysters, non-oyster bivalves, and mud crabs or the quantity of cultch shell deployed (Table 2). A marginally significant ($p = 0.065$) positive response however was observed between black drum detections and bivalve densities. All three species displayed negative relationships between mean daily detections and densities of live oysters.

Discussion

Identifying functional relationships between fish and their habitat is a fundamental component highlighted in ecosystem-based management, yet it is very challenging to accomplish (Caddy 2014). Utilizing telemetry approaches to monitor the behavior and habitat choices of three ecologically key and economically prized fishes provides valuable information regarding how estuarine organisms respond to the addition of man-made oyster reef habitat in a temperate estuary. The three fishes monitored in this study did not display any distinguishable behavioral preference for the enhancement reefs, and in fact, black drum and southern flounder on average spent more time at the non-enhanced reference sites, contradicting expectations that tagged fishes would be attracted to enhanced biogenic structure and associated fauna compared to nearby non-structured habitat. These findings do suggest that shellfish enhancement reefs may not serve as superior functional habitats for mobile, structure-associated fishes following destructive harvest for oysters, despite the persistence of remnant reef material. Although the same patterns held true for red drum and southern flounder when monitoring time spent at AR-

398, black drum expressed a notable preference for the restoration site defined by high relief structure over a relatively large spatial footprint. Overall, we hypothesized that all three fish species would have spent more time at the man-made enhancement and restoration sites in the NRE. The fact that observations generally did not meet these expectations challenges the notion that oyster reef habitat aggregates mobile fishes and serves as hotspots of species interactions and trophic transfers (although we readily acknowledge that these are dynamics we did not directly test).

Owing to studies over the last few decades identifying positive relationships between oyster reef habitat and nekton densities (*sensu* Peterson et al. 2003 and Humphries and La Peyre 2015), nearly all reef building efforts highlight positive linkages vis-avis secondary and tertiary production to support these projects. Specifically, reef enhancement programs, such as those deploying cultch shell designated for future harvest, reference all potential ecosystem benefits in project objectives regardless of the limited understanding of how harvesting practices can disturb oyster reef form and function. Man-made oyster reefs can develop into healthy habitats supporting faunal communities comparable to natural reefs as early as 12 months post-creation (Fodrie et al. 2014); however, degradation of the reef structure resulting from harvest practices can disrupt community dynamics, food web structure, and delivery of ecosystem services and function (Lenihan and Micheli 2000). Although the enhancement sites contained common reef associated macrofauna, small changes in abundance of potential forage species and trophic structure on the reefs resulting from altered structural complexity may be enough to reduce preference by higher order transient species like those monitored in this study.

A fundamental challenge in understanding the function of oyster reef habitat is identifying pattern and process at different scales (*sensu* Levin 1992). The small footprint of the

enhancement reefs monitored in this study (max = 10 acres) may limit their role as functional habitat that attracts large mobile fishes in the NRE following destructive harvest for oysters. Notably, two of the species monitored (black drum and southern flounder) displayed positive relationships between mean daily detections and relative size (# bushels of cultch shell) of the enhancement reef suggesting that larger reefs may be more suitable for attracting a greater variety of nekton (e.g., large mobile fishes). Previous studies have also found that habitat size (area) is a key factor in explaining community composition responses to changes in habitat structure and configuration (Yeager et al. 2016). Larger reefs may be more resilient to the negative consequences of oyster removal and overall changes in habitat structure associated with commercial harvesting practices allowing them to persevere in delivery of ecosystem services (e.g., provision of habitat). In fact, Beck and La Peyre (2015) found similar resident nekton communities at harvested and non-harvested sites in Louisiana at sites approximately 1.4x to 11.1x larger than the NRE cultch reefs. Additionally, the value of adding more oyster reef habitat in the NRE may be more discernable at the estuarine scale rather than at the scale of individual reefs. Meynecke et al. 2007 showed that quantity and diversity of habitat within individual estuaries can influence distribution and abundance of fish at regional scales where discernable value benefits are not visible at the local scale. Generating a broader spatial and temporal understanding of how target fish species use man-made habitats will allow more concerted and effective conservation approaches moving forward.

Successful construction of man-made habitats designated to benefit fish populations requires a clear understanding of the scale of fish movement and the spatial distribution of created habitats. Cultch reef enhancement sites within the NRE are primarily located in the lower region of the estuary (i.e. down river of the Hwy. 172 bridge) (83% of sites); however, fishes in

our study spent the majority of their time in the middle region of the NRE. The central and upper regions of the NRE are more characteristic of riverine habitats comprising shallow flats along the fringes, more creek outflows, and little high complexity structured habitat. With little overlap in the range of primary activity and spatial extent of enhanced sites in the NRE, in addition to the greater ratio of alternative suitable habitat (e.g., saltmarsh and creek outflows), mobile fishes may simply be less dependent on subtidal oyster reef resources in this estuary. Additionally, utilization of biogenic habitat by estuarine nekton is often dependent on the landscape characteristics surrounding the habitats of interest (Grabowski et al. 2005, Baillie et al. 2015, Ziegler et al. 2018). Nevins et al. 2014 suggested that the distance of subtidal oyster reefs from vegetated (e.g. saltmarsh) habitat may limit use by transient fish species. This may be a contributing factor in the NRE where man-made subtidal oyster reefs are typically > 200 meters from nearby shorelines. Notably, out of all the detections from the lower region of the river, we identified more activity at our site in Courthouse Bay which is a semi-enclosed bay with an abundance of shallow subtidal enhancement sites within close proximity (<100m) to fringing saltmarsh habitat. Landscape context (e.g. depth and proximity to marsh shoreline) as well as geolocation within the NRE may be more influential in how often select species may use these man-made habitats in the NRE (Nevins et al. 2014 and Grabowski et al. 2005).

Habitat selection by marine fishes is contingent on the availability and distribution of resources needed to maximize fitness (Shepherd and Litvak 2004). The distribution and abundance of food resources in the NRE could explain several of the patterns of habitat selection observed for the fish monitored in this study. Black drum in particular have been documented consuming large quantities of oysters on subtidal oyster reefs in the Gulf of Mexico (Brown et al. 2008, George et al. 2008); however, there were no clear relationships between live oyster

abundance at the cultch enhancement sites and daily detections of black drum. Positive relationships however were observed between black drum daily detections and densities of bivalves and mud crabs at all sites (cultch and reference). Both prey items have been identified in the diets of juveniles (similar in size to our study fish) in the Gulf of Mexico (Brown et al. 2008, George et al. 2008). The greatest bivalve (hard clam and surf clam) densities occurred at cultch reference sites. Furthermore, large quantities of mussels, also found in diet studies for black drum, were observed on marl pieces excavated from AR-398. These resource distributions may in part explain the daily detection disparities between site types monitored in the NRE. Although diets of red drum and flounder include forage species commonly associated with oyster reef habitat, resource acquisition for these fish may be greater at alternative habitats within the NRE (e.g. fringing shoreline marsh and small creek mouths). Diets of red drum in the NRE indicate the primary food resources are decapod crustaceans, penaeid shrimp, and Atlantic menhaden which occur within all habitats available in the NRE (Facendola and Scharf 2012).

Our findings within this single study mirror the range of past findings regarding linkages between subtidal oyster habitat and transient fishes, which viewed collectively are somewhat equivocal. Examples of functional habitat subsidies (Scyphers et al. 2011, Brown et al. 2014, Dillon et al. 2015) and habitat redundancies (Grabowski et al. 2005, Geraldi et al. 2009) are both common in the restoration ecology literature. Significant increases in nekton biomass and richness associated with oyster reef habitat have largely been highlighted in research on intertidal reefs (Grabowski et al. 2005, Ziegler et al. 2018) or have focused on resident nekton species (Lehnert and Allen 2002, Tolley and Volety 2005, Coen et al. 2007). Exploration of transient fish has produced mixed results with some studies identifying greater quantities of select species at subtidal reef habitats (Robillard et al. 2010) while others have found indiscernible catch

patterns between reefs and nearby unstructured habitats (Gregalis et al. 2009, Pierson and Eggleston 2014). These results support a growing consensus that the linkages between man-made subtidal oyster habitat and transient fish species are complex, and that quantitative relationships underpinning “essential fish habitat” warrant further development.

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TABLES

Table 4.1 Location and quantity of cultch material at six cultch oyster reef habitats where hydrophones were located in the New River Estuary.

Station	Latitude	Longitude	Description	Cultch Amount (# bushels)
19	34.61114	-77.41568	North Stones Bay	29095
20	34.59908	-77.43503	Stones Bay Middle	8050
24	34.58883	-77.36793	Courthouse Bay	8340
28	34.55588	-77.36723	Hatch Point	14817
29	34.55996	-77.34738	Traps Bay	19150
30	34.53024	-77.37393	Chadwick Bay	18056

Table 4.2 Results from regression analysis exploring the relationships between fish habitat use (detections·day⁻¹) and densities of select macrofauna (individuals·m⁻²) as well as quantity of cultch material deployed (# bushels). Relationship indicates the response direction of respective factors for each individual fish species and all species combined.

Metric	All Species			Black Drum			Red Drum			Southern Flounder		
	R ²	P-value	Relationship	R ²	P-value	Relationship	R ²	P-value	Relationship	R ²	P-value	Relationship
Bivalves	0.06	0.260	positive	0.15	0.065	positive	< 0.01	0.790	neutral	< 0.01	0.800	neutral
Live Oysters	0.12	0.094	negative	0.05	0.310	negative	0.05	0.260	negative	0.05	0.280	negative
Mud Crabs	0.01	0.860	neutral	0.56	0.140	positive	0.26	0.380	negative	<0.01	0.940	neutral
Cultch Material	0.07	0.610	positive	0.45	0.140	positive	0.23	0.340	negative	0.12	0.500	positive

FIGURES

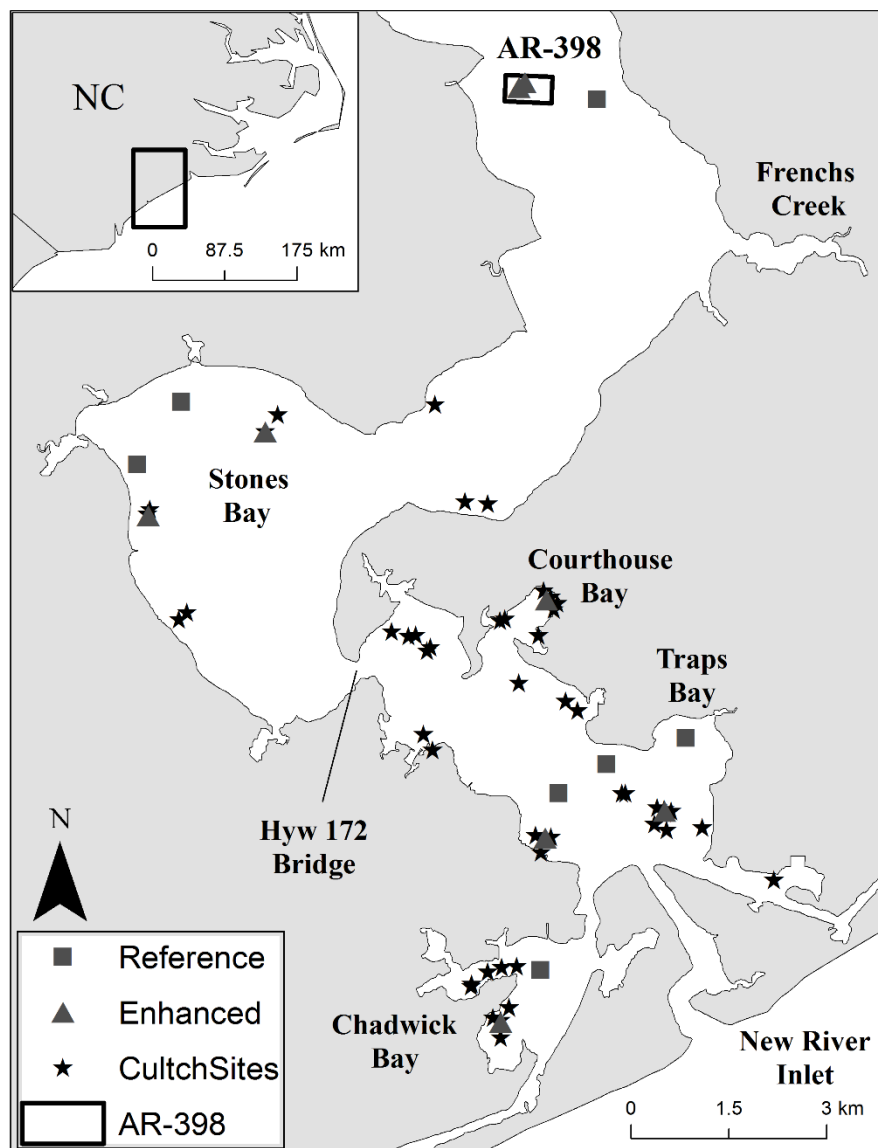


Figure 4.1 Map of the hydrophone observation network and location of man-made-made habitats monitored in the New River Estuary.

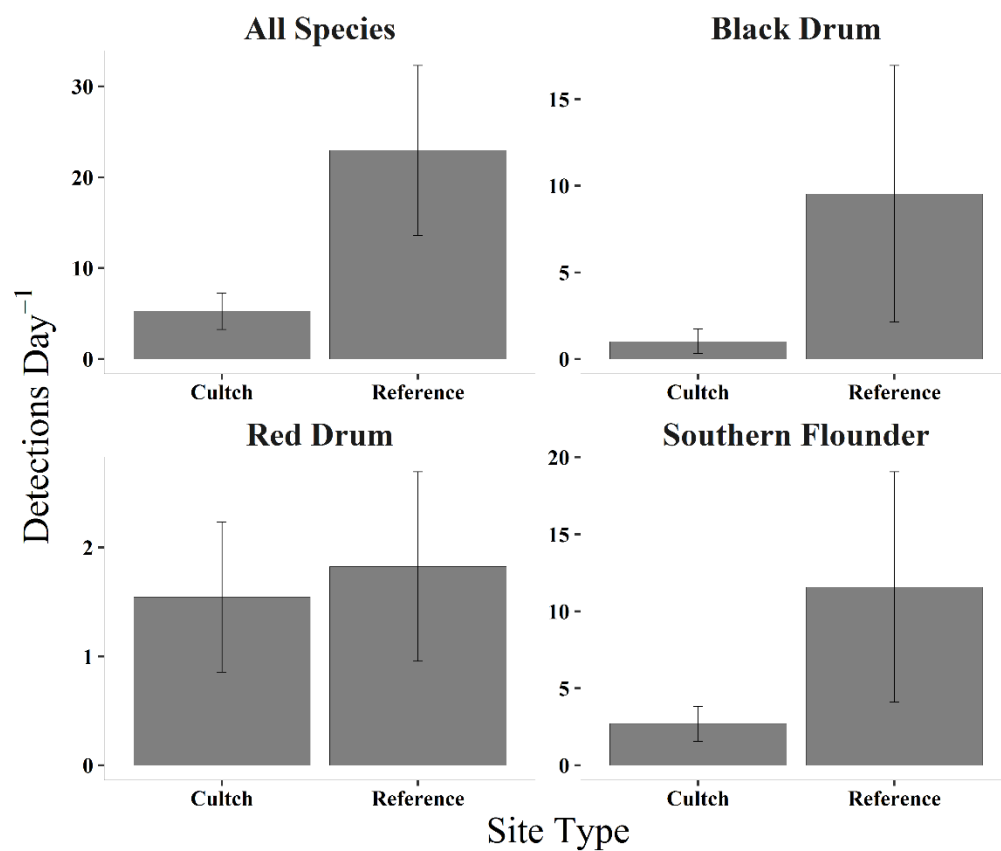


Figure 4.2 Mean number of detections day^{-1} at oyster cultch reefs and associated reference sites for each individual species and all species combined. Data are shown as mean ± 1 standard error.

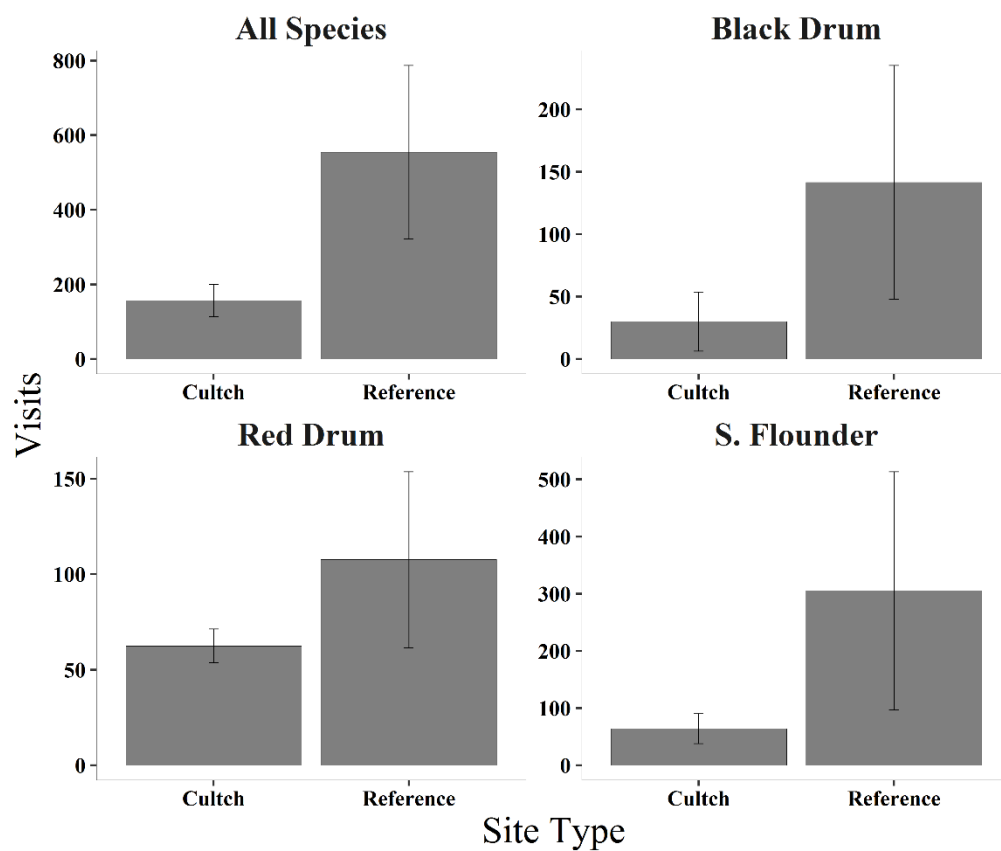


Figure 4.3 Mean number of detections day⁻¹ fish⁻¹ at AR-398 and the associated reference site for each individual species and all species combined. Data are shown as mean $\pm$ 1 standard error.

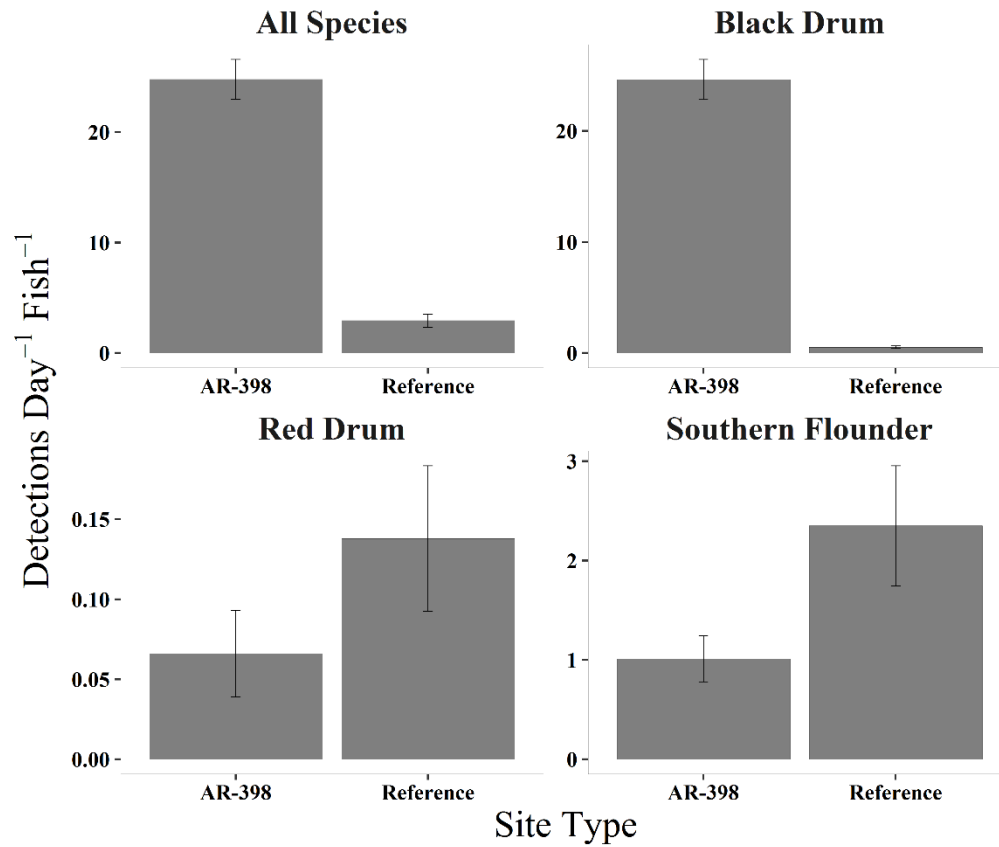


Figure 4.4 Mean number of total visits at oyster cultch reefs and associated reference sites for each individual species and all species combined. Data are shown as mean $\pm$ 1 standard error.

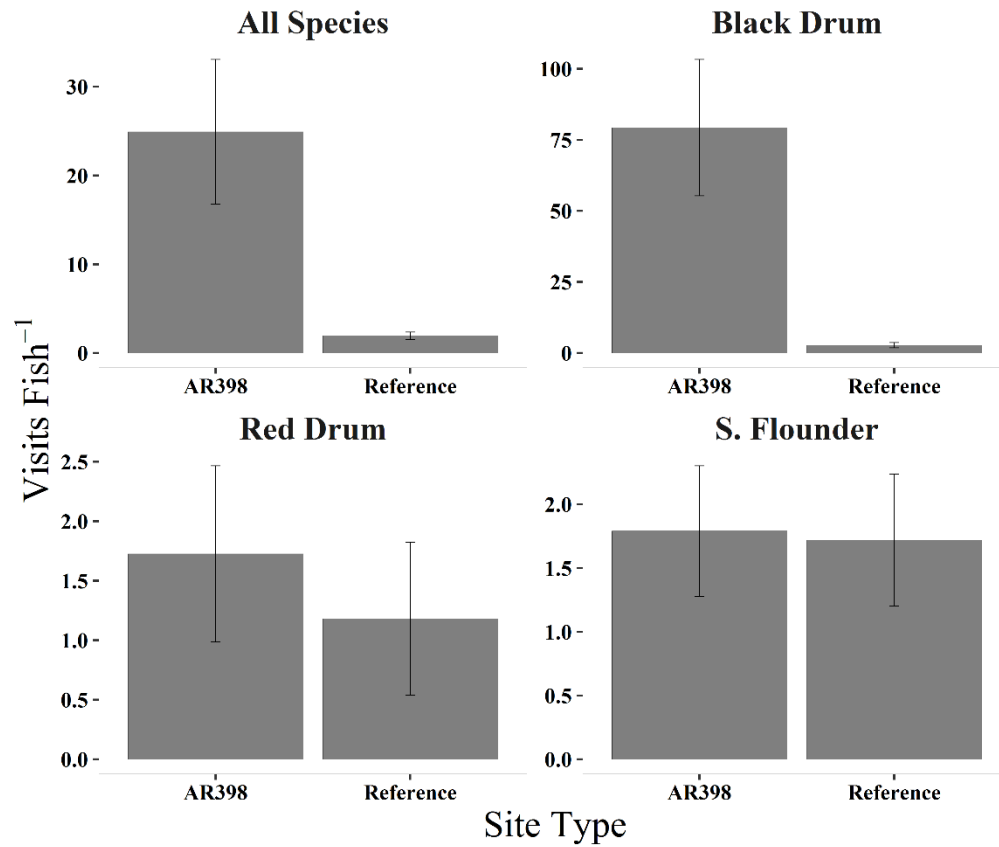


Figure 4.5 Mean number of total visits fish⁻¹ at AR-398 and the associated reference site for each individual species and all species combined. Data are shown as mean $\pm$ 1 standard error.