

ABSTRACT

RUDERSHAUSEN, PAUL JOSEPH. Nekton Population and Community Responses to Habitat and Urbanization Effects in North Carolina Tidal Creeks (Under the direction of Drs. Jeffrey A. Buckel and Joseph E. Hightower).

The southeastern United States coastline is experiencing rapid human development. Recognizing potential impacts from an expanding human footprint, the U.S. Environmental Protection Agency and North Carolina Division of Marine Fisheries have called for more scientific information to understand landscape-level anthropogenic impacts to fishes and crustaceans in the state's estuaries. I researched nekton community and population-level responses to habitat and anthropogenic effects in first-order tidal creeks in coastal North Carolina; it is these headwater systems that are most likely to show responses to anthropogenic impacts due to their proximity to land-based development. I found that creek-wide nekton communities changed from those dominated by resident species in less impacted systems to those dominated by transient species in systems that had lost marsh due to instream development and associated increasing water depth. At small (within-creek) spatial scales the nekton community responded to fragmentation; sites with anthropogenically deepened waters and conversion of marsh habitat to armored shoreline had declines in the relative contribution of marsh residents and were dominated by transient species. The dominant resident fish species from community analyses, *Fundulus heteroclitus*, had a lower probability of moving to sites impacted by development. The use of passive integrated transponder (PIT) tags was investigated in *Fundulus heteroclitus* to determine whether these tags could be used to estimate demographics of creek populations of this species. PIT tags were successfully implanted in adult *Fundulus heteroclitus* and tagged individuals were resighted with custom-built autonomous detection gear that allowed tidally-mediated

movement patterns to be determined and apparent survival to be estimated in a tidal creek. This work was followed with research using PIT tags as a tool across a gradient of habitat types and instream impacts to determine rates of apparent survival and densities of adult *Fundulus heteroclitus* in multiple tidal creeks. Modeling revealed that rates of apparent survival were similar across creeks and watersheds with different levels of development but that creek-wide densities were greater in creeks that retained greater percentages of marsh. Finally, rates of areal production of larval/juvenile *Fundulus heteroclitus* within salt marsh habitats were estimated across creeks with different creek-wide and watershed characteristics. The percentage of salt marsh across full high tide wetted areas of creeks and percent watershed imperviousness were not important explanatory factors of areal production within the marsh, indicating the ability of this species to maintain areal rates of production specifically within marsh habitats despite landscape-level alterations in tidal creeks in this region. Rates of larval/juvenile *Fundulus heteroclitus* production extrapolated to high tide wetted areas of creeks were positively related to adult abundances in September of each year of sampling, suggesting that increased larval/juvenile production is the likely mechanism for more adult *Fundulus heteroclitus* in creeks with higher creek-wide percentages of marsh. Taken overall, the results of this dissertation research suggest that loss of marsh, shoreline armoring, and increasing water depths – all common anthropogenic impacts to tidal creeks in the southeastern United States - will alter nekton communities and decrease densities of a trophically dominant nekton species in these systems.

Nekton Population and Community Responses to Habitat and Urbanization Effects in North
Carolina Tidal Creeks

by
Paul Joseph Rudershausen

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APPROVED BY:

Dr. Jeffrey A. Buckel
Committee Chair

Dr. Joseph E. Hightower
Committee Co-Chair

Dr. James A. Rice

Dr. Brian J. Reich

Dr. Benjamin H. Letcher

DEDICATION

To Muriel E. Rudershausen and Charles G. Rudershausen. They instilled in me my appreciation for the natural world long before I knew Henry Beston eloquently spoke of it in *The Outermost House*; “I lived in the midst of an abundance of natural life which manifested itself every hour of the day, and from being thus surrounded, thus enclosed within a great whirl of what one may call the life force, I felt that I drew a secret and sustaining energy.”

BIOGRAPHY

I am an ardent outdoorsman and adventurer with bachelors and masters degrees from the University of Maine and College of William and Mary, respectively. I have had a lifelong interest in publicly held resources and this interest has been strengthened by a dramatic increase in human impacts to coastal zones and impacts to stocks of commercially and recreationally exploited species in both fresh- and salt waters.

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CHAPTER 1. INTRODUCTION

Ecologists increasingly believe that landscape ecology - the study of relationships and interactions among landscape elements and changes to these processes due to natural and anthropogenic forces (Schlosser 1991; Grober-Dunsmore et al. 2009) - should account for both terrestrial and aquatic environments due to the connectivity between the two zones (e.g., Swanson et al. 1988; Wiens 2002). This is particularly true for salt marshes, which are transitional ecosystems that link terrestrial and aquatic habitats (Naimen and Décamps 1997) and provide ecosystem services in coastal zones that include water filtration, nutrient removal, and essential fish habitat (Décamps 1993; Naimen and Décamps 1997; Deegan et al. 2012). The concept of landscape ecology is important in tidal creek research because creek health is best viewed in the context of watersheds that hold them (Holland et al. 2004; Lowe and Peterson 2014; Krebs et al. 2014) and because nekton in creeks can be influenced by human impacts operating over multiple spatial scales (Van Dolah et al. 2008; Uphoff Jr. et al. 2011; Valesini et al. 2014).

Habitat-related research to aid U.S. coastal zone management has advanced the understanding of how environmental and habitat quality impacts biological communities but lags in understanding the relationship between fish population dynamics and the influence of landscape-level factors (Able 1999; Paul and Meyer 2001; Rice 2005). This is a gap in ecological research because anthropogenic impacts are recognized as a major force underpinning ecological pattern in estuaries (Bertness and Silliman 2008; Peterson and Lowe 2009) and because the biological consequences of land cover change is a research priority in landscape ecology (Wu and Hobbs 2002). Changing land use has been identified as a threat

to fish production in estuaries (e.g., Holland et al. 2004; Bilkovic and Roggero 2008; Partyka and Peterson 2008; Uphoff Jr. et al. 2011) and is a factor in the selection of ‘strategic habitat areas’ (SHAs) in North Carolina’s estuaries (Deaton et al. 2006). Some of these North Carolina SHAs include salt marshes, imperiled habitats along the U.S. coastal zones (Kennish 2001); due to their proximity to land-based runoff and landform changes they are more strongly affected by terrestrial inputs than more seaward habitats (Lerberg et al. 2000; Holland et al. 2004; Rabalais et al. 2009).

By targeting SHAs such as salt marshes for enhanced protection and restoration, the state of North Carolina recognizes that estuarine health is based on an interdependent relationship among the estuarine habitat types targeted for protection, anthropogenic alterations, and the distribution of estuarine fishes and crustaceans in these habitats (Jensen et al. 2014). However, vague boundaries between estuarine habitats (Halley 2005) coupled with the patchiness of habitats in urbanized areas (Grimm et al. 2008) makes the determination of human impacts on fisheries resources challenging in developing landscapes (Paul and Meyer 2001). Because responses to anthropogenic stressors can differ among biological communities and species (Brown et al. 2009; Krebs et al. 2014) and since disturbances are heterogeneous across landscapes (Resh et al. 1988; Turner 1989), a composite research program into habitat and anthropogenic influences in estuaries ideally estimates both population demographics and community structure to determine their relationships with habitat and environmental factors.

Information to guide management decisions on anthropogenic impacts should satisfy three criteria: be quantitative, site-specific, and characterize at least one biological community (Bilyard 1987). The estimation of demographics in dynamic habitats benefits

from sampling over time scales spanning multiple generations and across multiple life stages (Persson and Diehl 1990). Multi-scale sampling in creeks (Cooper et al. 1998) may allow more robust predictions of ecological pattern (Poff 1997). This dissertation study considers the aforementioned quantitative-, site-, and community-level criteria in undertaking research on nekton communities, movement, and fish demographics across multiple study creeks and sample sites in coastal North Carolina.

Chapter 2 of this dissertation examines nekton community structure at creek-wide spatial scales in six first-order tidal creeks in North Carolina using data collected by both active and passive sampling gears. For each gear type, non-metric multi-dimensional scaling coupled with a nonparametric dissimilarity-based method examined habitat and anthropogenic factors as well as nekton taxa that contributed to differences in community structure among study creeks.

Landscape connectivity influences the extent of movement of a species among habitat patches (Taylor et al. 1993). Loss of connectivity (fragmentation) represents a global threat to biodiversity (Collinge 2009). However, despite the importance of fragmentation as a contemporary ecological issue, the manifestations of it on estuarine nekton remain largely unknown (Minello and Rozas 2002). Chapter 3 of the dissertation examines nekton community structure at within-creek spatial scales to determine whether fragmentation of salt marshes as well as other anthropogenic factors affect community composition in first-order tidal creeks and rates of fish movement between closely spaced sites. This study involved sampling at fixed sample sites located on each side of crossings in ten tidal creeks; nine of these crossings possessed road culverts while one was a reference crossing (no culvert).

Chapters 2 and 3 identified *Fundulus heteroclitus* as a dominant tidal creek species that responded to common metrics of anthropogenic disturbance at both creek-wide and within-creek (creek reach) spatial scales. My goal was to estimate demographics of this species given its importance to nekton community structure in tidal creeks in which the community analyses were conducted. Estimating fish demographics helps to identify important estuarine fish habitats and determine biological responses to human impacts relative to collecting simpler data (e.g., presence/absence data) (Able 1999).

Estimating demographics of fish and wildlife populations has been aided by advances to tag and tag detection technologies. The use of passive integrated transponder (PIT) tags is one example of a recent research tool in saltwater environments that permits demographic and ecological data to be collected more regularly and over finer time scales compared to traditional gear types (Adams et al. 2006; Hering et al. 2010; Barbour et al. 2012). PIT tags and associated detection arrays allow researchers to obtain more precise estimates of some demographics, including survival, relative to traditional mark-recapture techniques (Hewitt et al. 2010). Chapter 4 investigates the feasibility of surgically implanting PIT tags in small-bodied *Fundulus heteroclitus* and autonomously detecting these tagged fish in saltwater creeks.

The use of any marking technique assumes that it does not influence the biological parameter of interest. In the case of using PIT tags to individually identify *Fundulus heteroclitus*, it was found in a lab study conducted at the outset of this dissertation research that these tags did not negatively affect survival or growth relative to untagged conspecifics, and that tags were not shed (Brewer et al. 2016). With this knowledge regarding the lack of a negative effect of PIT tags on survival, Chapter 5 of the dissertation proceeded to estimate

demographics of *Fundulus heteroclitus*, the trophically dominant species in U.S. Atlantic salt marshes (Kneib 1986). *Fundulus heteroclitus* is a model bio-indicator based on published attributes of such species (Hellowell 1986; Jones and Kaly 1996) due to a small home range size and residency to tidal creeks (Teo and Able 2003). The study presented in Chapter 5 estimated apparent survival and abundance of *Fundulus heteroclitus*, using PIT tags as a research tool, and related these demographics to habitat and anthropogenic factors measured at the creek- and watershed levels.

Biological production is a composite indicator of ecological health in estuaries (Able 1999) because it integrates population vital rates such as growth, mortality and abundance. Chapter 6 of the dissertation calculated production rates for individual cohorts of age-0 *Fundulus heteroclitus*, the dominant age class in terms of production in salt marshes (Teo and Able 2003). This work across a gradient of instream and watershed-level impacts found that component metrics of biological production – somatic growth and density - widely overlapped among five creeks despite one of them having lost a substantial percentage of its historical marsh area due to development.

Taken in sum, the results of this research study suggest that common types of instream development in tidal creeks in this region will reduce marsh percentage and connectivity among marsh patches, and thus affect community structure, species abundance, and movement patterns. However, the influence of watershed imperviousness – viewed as a composite metric of landscape-level human impacts to freshwater creeks (Wang et al. 2001; Brabec et al. 2002) and saltwater creeks (Holland et al. 2004; Krebs et al. 2014; Sanger et al. 2015) – was less clear. While it influenced creek-wide nekton community composition (Chapter 2), increasing watershed imperviousness did not influence rates of apparent

survival, abundance or production of *Fundulus heteroclitus*. These findings should give coastal land regulators hope that if critical salt marsh habitat is preserved through alternate development strategies (e.g., Currin et al. 2010; Gittman et al. 2016) that biological production of tidal creeks can be maintained despite watershed-level changes to landforms.

The U.S. South Atlantic coast is developing rapidly (Terando et al. 2014). Given the expanding human footprint in this region and species-specific responses to urbanization in saltwater creeks and their watersheds (Krebs et al. 2014), studies into the human impacts on other important resident and transient estuarine species are needed. The results of these types of studies will allow natural resource managers to use these relationships as guidance in habitat preservation and restoration efforts (Dahlgren et al. 2006).

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CHAPTER 2. COMPARISON OF FISH AND INVERTEBRATE ASSEMBLAGES AMONG VARIABLY ALTERED TIDAL CREEKS IN A COASTAL LANDSCAPE

Paul J. Rudershausen, Jeffrey A. Buckel, Marissa A. Dueker, Stephen J. Poland, and Ernie Hain

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ABSTRACT

We sampled variably altered tidal creeks to determine community structure in a developing coastal landscape. Throw trapping collected smaller and juvenile nekton in the vegetated marsh while minnow trapping in non-vegetated channels targeted relatively large fishes. Non-metric multidimensional scaling ordinations were used to assess community structure. Environmental factors and species that were most rank-correlated with community dissimilarities in ordinations were determined through the nonparametric dissimilarity-based 'BIOENV' analysis. We found differences in community composition among creeks that were largely consistent between the two years. For invertebrates captured in the throw trap, *Palaemonetes spp.* and *Callinectes sapidus* were part of the community in two creeks differing in anthropogenic alterations including increased watershed imperviousness and decreased marsh coverage. Juveniles of the dominant salt marsh fish *Fundulus heteroclitus* from throw trapping had a pattern opposite of amphipods and associated with creeks having marsh downstream while larger *Fundulus heteroclitus* (from minnow trapping) associated with creeks with high percentages of marsh coverage and lower watershed imperviousness. A transient fish *Lagodon rhomboides* was associated with creeks with lower marsh percentages. Results indicate that loss of marsh and breaks in marsh connectivity to areas

downstream of tidal creeks can lead to reduced abundances of a dominant resident marsh fish. In order to maintain production of marsh fishes, planners should prioritize the maintenance of intact salt marsh habitats and natural landforms.

INTRODUCTION

Salt marshes provide ecosystem services such as contaminant filtration, nutrient sequestration, and buffering from storm surge (Odum 1970; Costanza et al. 1997; Portnoy et al. 1999; Holland et al. 2004; Barbier et al. 2011). These biologically productive areas also provide vital habitat for resident nekton (Weinstein 1979; Kneib 1997; McIvor and Odum 1988; Teo and Able 2003; Bretsch and Allen 2006) and larger predators that forage in tidally flooded marshes (Minello et al. 2003; Rozas et al. 2007). Salt marshes are geographically positioned in coastal landscapes such that they link physical and chemical processes between upland areas and open-water estuaries (Holland et al. 2004; Sanger et al. 2015) as well as relay production to higher trophic levels in more seaward waterbodies (Teal 1962; Kneib 2000).

Anthropogenic impacts are known to impede the ability of estuaries to serve as nurseries for resident and transient fish species (Hinrichsen 1998). In the United States coastal zone, development is increasing 300-600% faster than the human population (Beach 2002) and over half of U.S. salt marshes have been lost, mostly due to human disturbance (Kennish 2001). Human encroachment also threatens the connectivity of these habitats (Kennish 2001; Thrush et al. 2008; Lowe and Peterson 2014) and biological production along the U.S. Atlantic and Gulf of Mexico coastlines (Dame et al. 2000; Seabrook 2012; Krebs et al. 2014a, Krebs et al. 2014b, Lowe and Peterson 2014). Due to displacement from habitats and physiological stress (Sklar and Browder 1998), estuarine nekton assemblages tend to

exhibit lower biomass and different community structure in environments that have experienced greater impact.

Among estuarine habitat types, tidal creeks may be particularly threatened by human development due to their proximity to uplands that they drain (Sanger et al. 2015; Krebs et al. 2014b). First-order tidal creeks are apt to show the strongest and most direct biological response to development because they are geographically the most immediate repositories of land-based contaminants (Sanger et al. 1999a, Sanger et al. 1999b, Lerberg et al. 2000; Van Dolah et al. 2008; Sanger et al. 2015). Specific anthropogenic impacts to tidal creeks include watershed development and imperviousness (Holland et al. 2004; Bilkovic and Roggero 2008), shoreline armoring that eliminates shallow-water habitat (Porter et al. 1997; Hale et al. 2004; Bilkovic and Roggero 2008; Krebs et al. 2014a), greater salinity fluctuations from freshwater pulses during rain events (Lerberg et al. 2000; Krebs et al. 2014a, Krebs et al. 2014b) and fragmentation of marsh habitats (Valentine-Rose et al. 2007; Eberhardt et al. 2011; Lowe and Peterson 2014). Because small tidal creeks receive runoff from neighboring terrestrial areas, they serve as sentinel systems by which to gauge cumulative anthropogenic impacts to estuaries (Holland et al. 2004; Sanger et al. 2015).

The relationship between specific, measurable anthropogenic alterations and metrics of nekton abundance remains poorly understood in tidal creeks (Partyka and Peterson 2008) and is less studied than similar impacts to freshwater creeks (Krebs 2014a, Krebs 2014b). For example, a recent synthesis of urbanization impacts to aquatic ecosystems did not cite any research into human impacts to saltwater creeks (Hughes et al. 2014). A small but growing body of evidence suggests that the biotic integrity of tidal creeks is affected by a suite of unique watershed and instream factors, some that are common to both freshwater and

tidal creeks, such as watershed imperviousness (Holland et al. 2004) and shoreline development (Bilkovic and Roggero 2008; Partyka and Peterson 2008; Lowe and Peterson 2014), but others that are unique to tidal systems and the fauna that use them, such as creek geomorphology (Allen et al. 2007). Compared to studies into impacts to benthic infauna in tidal creeks (Lerberg et al. 2000; Holland et al. 2004; Sanger et al. 2015), studies into impacts to nekton are less common. While research is emerging on the anthropogenic impacts to nekton in tidal creeks (Peterson and Lowe 2009; Krebs et al. 2014b, Lowe and Peterson 2014), further work is needed to strengthen the understanding of relationships between development and patterns of nekton abundance (Sanger et al. 2015). Characterizing biological communities is an effective approach for simultaneously measuring the response of multiple taxa to human stressors (Niemi et al. 2004). Furthermore, understanding how land use relates to patterns of nekton abundance in salt marshes is helpful information for projects intent on identifying and restoring the functional value of these productive habitats (Kneib 1997).

The objective of this study was to relate creek-wide fish and invertebrate communities to specific, measurable habitat and disturbance metrics in first-order salt marsh tidal creeks in a rapidly developing section of the southeastern U.S. coastline. We sampled variably altered systems possessing instream and watershed-level impacts representative of common residential and commercial disturbances along the U.S. Atlantic and Gulf of Mexico coastlines. Imperviousness exceeding 20% (Holland et al. 2004), 20-30% (Krebs et al. 2014a), and approximately 20-30% (Lerberg et al. 2000) in tidal creek watersheds has been used as a composite metric of impact and implicated in reducing biological diversity; several of our study creeks had imperviousness values exceeding these published threshold levels.

We hypothesized that more altered creeks would have different species assemblages than less impacted creeks nearby.

METHODS

Study Sites We sampled six first-order tidal systems in coastal North Carolina: Atlantic Veneer, Porters, Pelletier East, Pelletier West, Spooners, and Webb Creeks. These creeks spanned a gradient of habitat characteristics and alterations to their high tide wetted areas and watersheds (Table 2.1). Embedded in a landscape undergoing rapid development, the tidal creeks we studied epitomize the patchiness of estuarine habitats across spatially heterogeneous coastal landscapes (Boström et al. 2011). Across this landscape these creeks are positioned roughly equally with respect to semi-diurnal tidal inundation; the duration over which marsh flooding occurs around high tide is roughly the same among the five marsh-fringed creeks that we sampled.

Each study creek had a unique combination of environmental and habitat characteristics but also shared some characteristics with other creeks. All of the study creeks were considered polyhaline; high tide salinity at the downstream end of the sampled area of each creek is roughly 30 positive salinity units (psu) during non-rain periods. Atlantic Veneer, Porters, and Spooners Creeks are considered ‘rivulet’ marsh creeks in that shallow rivulets of water (~ 0.1 m deep) meander through part of each channel at low tide (Rozas et al. 1988; Hettler 1989). The full width of the channel of each of the other three creeks are largely covered with water over mean low tides. Except for Webb Creek, each creek has fringing salt marsh dominated by *Spartina alterniflora* (Loisel) (Figure 2.1; Table 2.1); Pelletier East Creek has the narrowest fringing marsh due to historic dredging that provided road fill. Each creek we studied had a different amount of intertidal-subtidal vegetated edge:

the linear distance of marsh edge that faces the creek channel. Each creek experiences semi-diurnal tidal amplitudes of roughly 1.0 m at its downstream end. Of the five salt marsh creeks that were sampled, none has any armored (bulkhead) shoreline within the sampling area; however, Pelletier East and Pelletier West Creeks have predominantly bulkhead shorelines with non-existent *Spartina alterniflora* coverage below the sampled area. In studies of tidal marsh production, the delineation of the downstream extent of habitat is often subjective (Kneib 2003). However, culverts can delineate boundaries of salt marshes for sampling (Stevens et al. 2006). We bounded the downstream sampling area by the presence of a culvert or a boundary with a higher order system. Upstream sampling was bounded by the most upstream extent of tidal influence or, in the case of Pelletier East Creek, an upstream culvert. Thus, except for Pelletier East Creek, each creek was sampled from the downstream mouth or culvert to the upstream extent of tidal influence.

Estimates of watershed and impervious surface areas Mapping and spatial analysis from ArcGIS (version 9.3.1) were used to estimate the watershed area of each creek and the percent of impervious surface within each watershed (Figure 2.1; Table 2.1). The primary data used for this analysis were digital elevation models (DEM) developed from light detection and ranging (LiDAR) data, field survey data, and aerial photographs. Watershed area for each study creek was estimated using the ‘watershed’ spatial analysis tool in the hydrology toolset in ArcToolbox®. Extraction of relevant features (hill slopes and flow paths) from the DEM layers was performed using the ‘flow direction’ tool, creating a new layer where flow direction and channeling points were represented. This layer was then used as the input for the ‘watershed’ tool which created a layer delineating watersheds for each study site. From this layer, watershed area (m²) for each study creek could be estimated from

the layer's attributes. Due to the low elevation of the study sites and minimal elevation change across the sites, the watershed delineation procedure in *ArcGIS* had trouble correctly assigning watershed boundaries for some creeks. Because of this, watershed layers were corrected by hand to conform to obvious contour changes in the landscape inferred from site visits and contour data layers. Recent satellite imagery from *Google Earth*® (images captured in 2010) was overlaid on watershed areas and used to estimate land use within the watershed. Impervious surface was estimated by manually drawing polygons over hardened (impervious) surface areas (i.e., buildings, driveways, walkways, and roads) within the watershed of each creek (Figure 2.1).

Fish and invertebrate sampling Tidal creeks were sampled from spring through fall in 2012 and 2013. Sampling over the bulk of the spring and summer provides the most representative characterization of nekton communities in shallow-water estuaries in this region (Bilkovic and Roggero 2008). Each creek was divided into ten evenly spaced strata that were sampled monthly with two different gear types: an actively deployed throw trap and passively deployed wire-mesh minnow traps. The throw trap targets small and juvenile fishes and epibenthic crustaceans (Rozas and Minello 1998; Turner and Trexler 1997) less than roughly 30 mm total length that use the marsh platform for foraging and refuge over most tides and that would not be retained by minnow traps if they elected to enter them. When adjusted for catchability (see below), throw trapping provides estimates of absolute densities of small fishes and invertebrates inhabiting salt marshes (Kushlan 1981; Rozas and Minello 1997). In contrast, minnow traps collect relatively large fishes (40 – 110 mm total length) (unpublished data) that typically make tidally-mediated migrations between vegetated and non-vegetated portions of salt marsh creeks (Allen et al. 2007). Sampling with both gears allowed us to

develop a more composite picture of both small- and large-bodied resident and transient fauna inhabiting multiple habitats in tidal creeks.

The throw trap was a 1 m² square by 0.6 m high aluminum frame with solid sides and an open top and bottom. The throw trap was deployed by foot in the marsh during high tide and used monthly in the five salt marsh creeks (but not in sub-tidal Webb Creek) by employing a stratified random sampling design. Distances upstream in each stratum and laterally into the fringing marsh, as well as the choice of left- vs. right-fringing marsh to sample, were randomly selected for throw trap sampling. We generally made ten throw trap deployments monthly in each creek, except in Pelletier East Creek, where the narrowness of the fringing marsh and steepness of the slope from the marsh to sub-tidal areas prevented trap deployment in roughly half of the strata (depending on high tide amplitude). Immediately after deployment, the trap frame was pressed into the sediment to prevent escapement of fishes and epibenthic crustaceans. Water depth was measured (± 0.1 m) and percent vegetation (*Spartina alterniflora* stem density) in the trap was visually estimated (nearest 10%) in conjunction with each deployment. Water temperature ($^{\circ}\text{C}$), salinity (psu) and dissolved oxygen concentration (mg/l) were measured in the lower, middle, and upper creek reaches during monthly throw trap- and minnow trap collections (below). We swept each throw trap deployment 50 times with a 0.30 x 0.25 m dip net made of 0.72 mm² mesh and initially removed vegetation (before subsequent sorting in the lab) by sieving each trap's sample through a wash bucket possessing 0.22 mm² mesh. All fauna and remaining organic matter were preserved in 95% denatured ethanol for subsequent identification and enumeration.

Our goal was to use throw trapping to estimate fish and invertebrate densities. Sampling bias, due to differing recovery efficiencies (Rozas and Minello 1997) (see below) for different species or environmental factors (e.g. vegetation density, water depth), may exist when researchers use actively deployed enclosure-type samplers (Kushlan 1981; Rozas and Minello 1997). To account for these potential biases, a subset of throw trap samples (collected in September 2013) was used to estimate species-specific recovery efficiencies across a range of water depths and vegetation densities. For each stratum sampled during this month we preserved each set of ten sweeps in a separate jar to determine the rate of decline of catch of each targeted taxon with each successive units of effort. This resulted in five jars preserved per throw trap deployment during this month (Sweeps 1-10, 11-20, 21-30, 31-40, and 41-50). Estimates of taxon-specific recovery efficiencies and environmental conditions from September 2013 samples were then used to develop models to estimate recovery efficiencies by taxon for all trap deployments made over the full study.

Gee-style wire mesh minnow traps (6.4 mm square mesh) baited with dried pet food were deployed in channels of each creek stratum for 3-hour soak times around high tide. Traps were deployed using a stratified random sampling design whereby distance upstream into each stratum to deploy each trap (by thirds) was randomly selected. We generally fished one minnow trap per creek stratum except for Porters Creek, where we fished two traps per stratum because of its relatively large size. We assumed independence among minnow trap deployments. Deployment of minnow traps in channels ensured that trap entrances remained submerged during high tide sampling and could be retrieved by boat at the conclusion of the 3-hour soaks. All minnow-trapped individuals were identified, counted, and released.

Data analysis: estimating absolute abundance from throw trap collections Catch efficiency (or catchability) relates absolute abundance to catch (Arreguín-Sánchez 1996). Throw trap catch efficiency has two components: gear capture efficiency and recovery efficiency (Rozas and Minello 1997). Gear capture efficiency is the proportion of targeted animals in an area that are enclosed by the trap while recovery efficiency is the proportion of animals recovered of those enclosed. We estimated absolute abundance, \widehat{N} , of common fauna collected by throw traps because we suspected that the catch after sweeping each throw trap 50 times did not recover all targeted individuals (recovery efficiency < 1). This approach required us to save and process samples of every ten successive sweeps for the depletion analysis. Given this laborious process, we only empirically determined absolute abundance and overall recovery efficiency ($q_{deployment}$) during September 2013. Additionally, the analysis was limited to four taxa collected by the throw trap (*Fundulus heteroclitus*, *Gambusia holbrooki*, *Palaemonetes* spp., and Amphipoda) in instances where we had a non-zero catch of each of these taxa in a trap. Non-zero trap catches for other species collected in September 2013 were not sufficiently high enough ($n > 10$) to estimate absolute abundance.

Absolute abundances of *Fundulus heteroclitus*, *Gambusia holbrooki*, *Palaemonetes* spp., and Amphipoda from throw trapping were estimated in several steps. First, we used the Leslie-Davis depletion estimator (Leslie and Davis 1939) to estimate density (\widehat{N}) for each September 2013 trap deployment. The depletion estimator was implemented in Program R (R Development Core Team 2011) using the *fishmethods* package (Nelson 2011). Catch data from the five successive units of effort (1 unit of effort = 10 net sweeps) were used to estimate q_{effort} , the recovery efficiency between successive units of effort. We then calculated overall recovery efficiency for each September 2013 trap deployment and taxon, $q_{deployment}$,

by dividing the cumulative catch over the 50 sweeps by the estimate of \hat{N} from each trap deployment. Thus, $q_{deployment}$ represents the cumulative recovery efficiency for a particular taxon after fifty sweeps of the net within the trap, and is synonymous with the term “efficiency” used for similar gear types commonly deployed in vegetated estuarine habitats (Kushlan 1981; Rozas and Minello 1997). Third, we used normally distributed general linear models to determine the relationship between $q_{deployment}$ and two potential covariates collected during throw trap sampling: water depth, percent emergent vegetation (*Spartina alterniflora*) in each trap deployment, and the interaction between these two factors. Plots of the raw data as well as post-hoc residual plots revealed no unusual patterns to contra-indicate the use of normal distributions for these model fits. Thus, five models of $q_{deployment}$, including an intercept-only model, were developed for each of the four taxa. We used Akaike Information Criteria (AIC; Burnham and Anderson 2002) to evaluate model parsimony and determine factors most influential on $q_{deployment}$. Checks of the dispersion parameter, \hat{c} , revealed that these data were not overly dispersed. Chi-square goodness of fit testing was used to assess the adequacy of model fit (if the probability level exceeded 0.05). We used results of best fitting models (determined through AIC) to calculate the $q_{deployment}$ for each main taxon in each trap deployment over the course of the full study. Finally, \hat{N} was estimated for each main taxon in each deployment over the full study by dividing catch of a taxon in each trap deployment by the estimated $q_{deployment}$ for that deployment. We could not estimate recovery efficiencies for less abundant species, given sample size constraints, and assumed that the catch of each of these less abundant species was representative of absolute abundance.

Data analysis for community assessment We tested whether creeks differed in community composition and determined environmental and habitat factors that explained differences in

creek communities by gear type. Non-metric multi-dimensional scaling (NMDS) was used to graphically depict fish and invertebrate communities of each creek. NMDS is an ordination technique for graphical representation of community relationships of non-normal or discontinuous data (Clarke 1993; McCune and Grace 2002). NMDS arranges samples so that the rank-order correlation between distance measures and distance in ordination space is maximized, while also minimizing stress: a measure of fit between ordination space and multi-dimensional space (McCune and Grace 2002). We conducted a separate NMDS ordination for each gear and year. The Bray-Curtis coefficient was used to construct similarity matrices for the sample-by-species matrix on counts of individuals from throw trap and minnow trap collections, which were square-root transformed to diminish the influence of numerically dominant taxa. To balance uniform exclusion versus inclusion of rare species (Poos and Jackson 2012), we elected to include species in each gear-specific NMDS that comprised at least 0.1% of the total abundance for that gear type (by year). Each individual sample by a gear type was considered a 'sample' for NMDS; however, deployments with zero data across all the taxa considered in the ordination (those > 0.1% in numerical abundance in our case) cannot be evaluated. For the throw trap data, NMDS was performed using estimated abundance, \widehat{N} , for the four taxa for which recovery efficiency was computed and using catch data for the other taxa that met the 0.1% inclusion threshold. NMDS for minnow trap collections was performed using catch data. Fit (stress) was computed as part of each gear-specific NMDS ordination to determine how well the Euclidean distances preserved Bray-Curtis sample dissimilarities (Kruskal 1964; McCune and Grace 2002): stress levels < ~ 0.2 are considered reasonable (Clarke and Warwick 2001). Relatively high stress values (> 0.2) can potentially lead to misinterpreting scaling distances (Clarke and Warwick

2001). An Analysis of Similarity (ANOSIM) procedure was conducted in conjunction with each NMDS to provide a quantitative interpretation of whether biological communities differed among creeks. The ANOSIM test statistic, R , varies from -1 to 1 but most typically from 0 to 1; increasingly more positive values indicate greater differences among sites while a value of 0 for R indicates no dissimilarities among sites (Chapman and Underwood 1999).

Urbanization to creek habitats includes factors that can be difficult to summarize (Wang et al. 2001). We measured numerous habitat and environmental factors at the creek and watershed levels to better characterize habitat types in and around each study system. We sought to determine the subset of environmental and habitat factors that were most related to differences in biological communities among creeks for each collection gear and year of data. This was done through the nonparametric BIOENV analysis (Clarke and Ainsworth 1993) that determines the suite of variables that possess the greatest rank correlation with sample dissimilarities. BIOENV can be conducted with environmental/habitat data as well as biological data; the latter can be used to determine the group of taxa that have the greatest rank correlation with sample dissimilarities. We conducted BIOENV analysis with each type of data, using a “forward selection/backward elimination approach” where the rank correlation in sample dissimilarities between a subset of environmental variables/taxa and the full data set of environmental variables/taxa was set at 0.95 (Clarke and Warwick 1998). Euclidean distances among sample items were calculated as part of each BIOENV procedure; this distance measure can be applied to both categorical and continuous environmental/habitat data (McCune and Grace 2002). A Spearman correlation coefficient (ρ) was calculated for the best-fitting suite of environmental/habitat factors and taxa, respectively.

BIOENV analysis allows environmental variables and taxa that are most correlated with sample dissimilarities to be plotted in NMDS ordination space. Each continuous environmental/habitat factor in the most parsimonious BIOENV model is plotted as a vector while each level of each categorical factor in the model is plotted as a point. Each taxon in the best fitting BIOENV analysis of biological data is plotted as a vector. Continuous environmental/habitat factors considered in the throw trap and minnow trap BIOENV analyses included percent watershed imperviousness, percent of each creek's high tide wetted area that was vegetated, water temperature, salinity, dissolved oxygen, and mean creek channel depth at bank-full level. We included mean creek channel water depth because it has been found to be an important geomorphological determinant of nekton use of tidal creeks in the southeastern U.S. coastal plain (Allen et al. 2007) and metrics of channel morphology (such as water depth) influence nekton movement through these corridors (Rozas et al. 1988; Visintainer et al. 2006; Allen et al. 2007; Boström et al. 2011). Categorical factors considered in each BIOENV analysis included stratum number (distance upstream: 1-10) as well as the presence/absence of 1) a culvert, and 2) contiguous marsh found immediately downstream of the creek's mouth or culvert. An additional factor incorporated into the throw trap BIOENV analysis included the lateral distance into the marsh (closest to the inter-tidal channel, in the middle marsh, or closest to the high marsh) where each trap deployment occurred. Shoreline armoring ('bulkheading') was a categorical factor only in the minnow trap BIOENV analysis because of the addition of Webb Creek (which had bulkheads within the sampled area) to that analysis. Standing water was considered a categorical factor in preliminary model runs but was eliminated from subsequent runs because of its strong negative correlation with the presence of marsh downstream. Water depth and percent

vegetation in each throw trap sample were not considered as environmental factors in the throw trap BIOENV analysis because they were considered in models of recovery efficiency (above). NMDS, BIOENV, and fitting of environmental variables and taxa groupings was done through the *R* package *vegan* using the *metaMDS*, *bioenv*, and *envfit* functions, respectively (Oksanen 2014). The *envfit* function was also used to evaluate the significance of each individual environmental/habitat factor included in each best fitting BIOENV model through a permutation test.

We ran follow-up univariate models after the BIOENV procedures in order to determine whether habitat and environmental factors that were most responsible for community differences among creeks influenced the abundance of dominant taxa that contributed to among-creek community differences. Each model that we constructed focused on predictor variables (habitat/environmental factors) and response variables (dominant taxa) that each year's BIOENV analysis for a gear type showed via loadings on ordination plots as contributing to community differences among creeks. Dominant taxa included *Fundulus heteroclitus*, *Cyprinodon variegatus*, *Lagodon rhomboides*, and combined density/catch data from *Palaemonetes* spp. and *Callinectes sapidus*. We elected to combine data from these two taxa of crustaceans due to the similar manner in which they loaded on throw trap ordinations (see *Results*). We compared the mean abundance of each main taxa for binary and continuous predictors. Each model included data from both 2012 and 2013. Comparisons with binary predictors used unpaired t-tests on untransformed data when a Bartlett's test did not reveal heterogeneity between group variances ($p > 0.05$) and on logarithmically transformed data ($\ln(x+1)$) when it did. Linear models regressing each taxon against a continuous predictor were conducted using logarithmically transformed catch data.

RESULTS

A total of 640 throw trap and 1,001 minnow trap deployments were made over the course of the study. Mean monthly water temperature and dissolved oxygen concentration generally overlapped among creeks during each of the two sampling seasons (Figures 2.2A-C). However, mean monthly salinity was generally lower in Pelletier East and Pelletier West Creeks than other creeks (Figure 2.2B). Mean (\pm S.E.) percent *Spartina alterniflora* coverage in throw traps, a proxy for stem density of this emergent vegetation, was 61.1 ± 0.5 , 65.2 ± 0.4 , 68.6 ± 0.3 , 72.4 ± 0.8 , and 80.6 ± 0.3 for Porters, Atlantic Veneer, Spooners, Pelletier East, and Pelletier West Creeks, respectively.

Fundulus heteroclitus, *Gambusia holbrooki*, *Cyprinodon variegatus*, *Palaemonetes* spp., and Amphipoda, all resident nekton to U.S. Atlantic coastal salt marshes (Kneib 1997), were the five most abundant taxa from throw trap samples and accounted for 96.3% of the cumulative catch from this gear type (Tables 2.2 and 2.3). *Fundulus heteroclitus*, *Gambusia holbrooki*, and *Cyprinodon variegatus* were three of the four most abundant species captured from minnow trap samples and accounted for 95.2% of the cumulative catch from this gear type (Tables 2.4 and 2.5). Transient taxa were caught in relatively low numbers by each gear; *Farfantepenaeus* spp. was the most abundant transient taxon caught in the throw trap and accounted for 0.8% of the catch while *Lagodon rhomboides* was the most abundant transient taxon collected from minnow traps and accounted for 4.3% of the individuals. The sizes of *Fundulus heteroclitus*, *Gambusia holbrooki*, and *Cyprinodon variegatus*, fauna common to both the throw trap and minnow traps, were smaller from throw trap samples than from minnow trap samples (Table 2.6).

Recovery efficiency ($q_{deployment}$), measured from September 2013 throw trap samples, was relatively high but differed among taxa. *Fundulus heteroclitus* and Amphipoda had a relatively lower mean (\pm S.D.) $q_{deployment}$ (0.88 ± 0.20 and 0.82 ± 0.22 , respectively) than *Gambusia holbrooki* (0.98 ± 0.07) and *Palaemonetes* spp. (0.99 ± 0.29). Covariates important to throw trap recovery efficiency differed among taxa. For *Fundulus heteroclitus*, $q_{deployment}$ was negatively related to the percentage of *Spartina alterniflora* while $q_{deployment}$ of *Palaemonetes* spp. was negatively related to increasing water depths (Table 2.7). *Spartina alterniflora* and water depth did not influence recovery efficiency of *Gambusia holbrooki* or Amphipoda (Table 2.7).

NMDS ordinations were respectively conducted on data from the 628 throw trap samples and 678 minnow trap samples that had non-zero catches. Eleven and thirteen taxa met the relative abundance threshold for inclusion into the ordination for throw trap collections in 2012 and 2013, respectively (Table 2.2). Four and six different taxa were included in the 2012 and 2013 minnow trap ordinations, respectively (Table 2.4).

There were differences in community assemblages among creeks (Figures 2.3 – 2.6). For throw trap ordinations, Porters and Atlantic Veneer Creeks separated out from the other three creeks which had more overlap in each year (Figures 2.3A and 2.4A). Minnow trap ordinations displayed less community overlap among creeks than throw trap ordinations; Pelletier East and Webb Creeks separated out from the other four creeks, which largely overlapped (Figures 2.5A and 2.6A). Webb Creek had the smallest ellipse.

ANOSIM results were consistent with visual assessments of ordination plots. There were significant differences in faunal assemblages for annual throw trap data (2012; $R = 0.258$, $p = 0.001$ 2013: $R = 0.182$, $p = 0.001$) and minnow trap data (2012; $R = 0.345$, $p =$

0.001 2013: $R = 0.393$, $p = 0.001$). Stress was 0.189 and 0.231 for 2012 and 2013 throw trap ordinations and 0.063 and 0.087 for 2012 and 2013 minnow trap ordinations, respectively. Thus, one ordination (2013 throw trap) had relatively high stress (> 0.2). However, we believe that this did not hinder our interpretation of the result due to the similarities in throw trap ordinations between the two years.

For each gear type, the suite of fish and invertebrate taxa that was most correlated with sample dissimilarities was consistent between years. The five numerically dominant taxa in the throw trap (Table 2.2), as well as *Callinectes sapidus*, were most correlated with sample dissimilarities for the throw trap ordination in 2012 (Figure 2.3B) and 2013 (Figure 2.4B). *Lagodon rhomboides*, *Fundulus diaphanus*, *Dormitator maculatus*, *Mugil* spp. and Xanthidae were additional taxa in the best fitting throw trap model for 2013 (Figure 2.4B). Best fitting BIOENV models for minnow trap ordinations in 2012 (Figure 2.5B) and 2013 (Figure 2.6B) included only two species: *Fundulus heteroclitus* and *Lagodon rhomboides*. Spearman ρ values were 0.847 and 0.803 for throw trap taxa correlations in 2012 and 2013, and 0.966 and 0.917 for minnow throw trap taxa correlations in 2012 and 2013. Trends among creeks in throw trap densities and minnow trap catches for each main species (Figure 2.7) were consistent with the ordination results.

For each gear type, the suite of environmental/habitat factors that showed the greatest rank correlation with sample dissimilarities was similar between years. The presence/absence of a culvert, the presence/absence of contiguous marsh downstream, and mean creek depth were in the best-fitting correlation with sample dissimilarities for the throw trap ordination in each year (Figures 2.3C and 2.4C). Percent watershed imperviousness and marsh percentage in each creek were factors in best fitting models for minnow trap

ordinations in each year (Figures 2.5C and 2.6C). The presence/absence of contiguous marsh downstream, salinity, and dissolved oxygen were additional factors in the BIOENV model that best fitted the minnow trap ordination in 2013 (Figure 2.6C). Permutation tests found that almost all individual environmental/habitat factors in the four best-fitting BIOENV models were significantly rank correlated ($p < 0.01$) with ordination sample dissimilarities for the respective ordination; the only exception was dissolved oxygen, which was not significantly correlated with ordination of 2013 minnow trap data ($p = 0.109$). Spearman *rho* values were 0.222 and 0.193 for throw trap environmental/habitat correlations in 2012 and 2013, and 0.540 and 0.576 for minnow throw trap environmental/habitat correlations in 2012 and 2013.

For each gear, the direction and strength of gradients for fish and invertebrate taxa (Figure 2.3B-2.6B) showed consistent trends with environmental/habitat gradients (Figure 2.3C-2.6C) across years. For invertebrates captured in throw trap samples, amphipods were an important contributor to creek dissimilarities, being more abundant in creeks that had no marsh downstream while *Palaemonetes* spp. and *Callinectes sapidus* were consistently a part of the community in two creeks that had little impact (Porters Creek) and extensive impact (Pelletier East Creek). The dominant fish across gears/years and included in best fitting BIOENV models, *Fundulus heteroclitus*, was most closely associated with creeks having high percentages of marsh, contiguous marsh downstream of the sampled area for small individuals caught in throw traps, as well as shallower mean channel depth and lower watershed imperviousness for large individuals caught in minnow traps. The transient fish *Lagodon rhomboides* (from minnow trapping) associated with creeks with lower percentages of vegetated marsh. This species loaded on 2013 throw trap and minnow trap ordinations

similar to mean channel water depth. Throw trapped *Gambusia holbrooki* and *Cyprinodon variegatus* were consistently related to sample dissimilarities in both years and predominantly found in two creeks possessing culverts (Pelletier East and Pelletier West) that lacked marsh downstream. These two species loaded on the 2013 throw trap ordination in a manner almost identical to mean channel water depth.

In follow-up univariate tests of species and environmental factors, we found that throw trapped *Fundulus heteroclitus* had a significantly greater mean abundance in creeks with marsh downstream ($t = -3.40$, degrees of freedom (df) = 626, $p < 0.001$) while the opposite was found for *Cyprinodon variegatus* ($t = 7.64$, df = 626, $p < 0.001$). The regression of combined abundances of throw trapped *Palaemonetes* spp. and *Callinectes sapidus* against water depth showed that the coefficient for water depth was significant (adjusted $r^2 = 0.096$, df = 626, $p < 0.001$). Finally, we regressed catches of minnow trapped *Fundulus heteroclitus* and *Lagodon rhomboides* against the percentage of marsh in the study creeks and found that the coefficient for percent marsh was significantly positive for the model that included *Fundulus heteroclitus* (adjusted $r^2 = 0.420$, df = 683, $p < 0.001$) and significantly negative for the model that included *Lagodon rhomboides* (adjusted $r^2 = 0.440$, df = 683, $p < 0.001$).

DISCUSSION

Differences in biological communities among saltwater creeks along the U.S. Atlantic and Gulf of Mexico coastlines have been related to human alterations (Holland et al. 2004; Krebs et al. 2014b, Lowe and Peterson 2014). However, variability about nekton density within a creek and among sampling seasons makes the detection of anthropogenic impacts difficult among creeks (Rose 2000; Ellis and Bell 2013). The performance of bio-indicators

of habitat condition in tidal creeks may be improved by accounting for spatio-temporal variation of fauna in these systems through the study sampling design (Shenker and Dean 1979; Talbot and Able 1984; Allen et al. 2007). In this study we sampled across tidal creeks possessing objectively measured habitat and physical attributes believed to be important to distributions of tidal creek nekton potentially impacted by disturbances (Stewart-Oaten 1996). Our sampling was consistent across sites, tides, and biologically productive seasons to help lessen the influence of spatial and temporal variability about nekton abundances on our interpretation of biological pattern. Using a multivariate ordination approach we found differences in community assemblages among creeks. These differences were largely consistent across the two years and that appear attributable to habitat and watershed characteristics. Some of these characteristics reflect anthropogenic impacts to tidal creeks in a developing landscape. Our multivariate analyses support the hypothesis that loss of marsh and severing the physical connectivity of marsh habitat to areas downstream in first-order tidal creeks can lead to reduced abundances of dominant resident nekton. Despite difference in sample gears, regions, and sizes of study areas, our results are consistent with recent Gulf of Mexico analyses that identified creek and watershed-level anthropogenic impacts as factors influencing nekton community composition in that region (Sanger et al. 2011; Krebs et al. 2014b; Lowe and Peterson 2014).

Ecosystem heterogeneity over space and time (Brown et al. 2004) is one of the dominant themes in ecology (Wu 2006). Such variability can mask the detection of environmental impact (Wiens 1989), particularly in dynamic habitats such as tidal creeks (Able 1999). Complicating the interpretation of ecological pattern is the fact that human impacts are not necessarily destructive from the organism's perspective; more heterogeneous

habitats are apt to provide a greater number of niches (MacArthur and Wilson 1967) and human disturbance can create spatial heterogeneity at multiple scales (Turner 2005). In this study we sampled across multiple temporal and spatial scales to attempt to account for ecosystem variability and determine ecological pattern. Our sampling effort produced relatively robust sample sizes over some scales (e.g., number of samples per creek) but low sample sizes over others (e.g., numbers of creeks that were sampled). We found that some factors were statistically meaningful covariates of community patterns. Increasing the sample sizes over some of the spatial scales or sampling a different suite of creeks may have revealed different or more apparent patterns than those that we observed, and may have helped to explain more of the variability in community patterns.

Urbanized tidal creeks have been characterized as having increased watershed imperviousness (Holland et al. 2004), reduced marsh coverage (Lowe and Peterson 2014), reduced or eliminated vegetated buffers (Uphoff et al. 2011; Krebs et al. 2014a; Krebs et al. 2014b), armored shoreline (Bilkovic and Roggero 2008; Lowe and Peterson 2014), and fragmented habitat due to infrastructure (e.g. culverts) (Porter et al. 1997; Eberhardt et al. 2011; Krebs et al. 2014a). We examined whether some of these urbanization factors – those that BIOENV analyses showed that created community dissimilarities among our study creeks - influenced patterns of nekton abundance and found that they did.

Community assemblages differed among the tidal creeks we sampled. Biologically speaking, these differences were largely driven by a limited number of species such as *Fundulus heteroclitus*, the dominant fish species in U.S. Atlantic coastal salt marshes (Kneib 1986; Kneib 1987). Estimated densities of small *Fundulus heteroclitus* from throw trap samples and catches of larger conspecifics from minnow trap samples were greater in creeks

with higher percentages of marsh, lower percentages of watershed imperviousness, and continuous marsh below creek mouths/culverts.

The dependency of *Fundulus heteroclitus* on *Spartina alterniflora* salt marsh is well established (Kneib 1984; Kneib 1986; Teo and Able 2003; Meyer and Posey 2009).

Fundulus heteroclitus is known to use salt marsh for foraging and refuge (Weinstein 1979; Kneib 1997; Rozas and Minello 1998; Teo and Able 2003; Allen et al. 2007) as well as reproduction (Taylor et al. 1977; Taylor et al. 1979). The percentage of vegetated marsh surface in creeks was a significant factor in minnow trap analyses and associated closely with *Fundulus heteroclitus* in ordination space. Our results associating this marsh resident with less altered habitats are consistent with those of Lowe and Peterson (2014) who found that a congener, *Fundulus grandis*, was more abundant in less urbanized Gulf of Mexico tidal creeks. Inter-tidal salt marsh surface is recognized for facilitating secondary production in tidal creeks (Boesch and Turner 1984; Kneib 2000; Teo and Able 2003) by providing enhanced refuge from predation and greater trophic support than non-vegetated channels (Kneib 1987; McIvor and Odum 1988; Kneib 2003).

Imperviousness is an integrated metric of urbanization in watersheds (Schueler 1994; Arnold and Gibbons 1996; Wang et al. 1997; Wang et al. 2001; Schueler et al. 2009; Coleman et al. 2011) that can lead to contamination in tidal creeks (Kennish 1991; Sanger et al. 1999a, Sanger et al. 1999b). Watershed imperviousness was a significant factors in minnow trap BIOENV models. Three study creeks (Pelletier West, Pelletier East, and Webb Creeks) lie in watersheds with imperviousness exceeding 20% (Table 2.1) and these were the least related to *Fundulus heteroclitus* abundance in both throw trap and minnow trap ordinations.

The presence of contiguous marsh downstream of sampled areas was also a factor that associated with *Fundulus heteroclitus*. This finding is consistent with the view that marsh configuration and structural connectivity, not merely presence/absence, is important in determining nekton patterns in tidal creeks (Partyka and Peterson 2008; Green et al. 2012; Lowe and Peterson 2014). Fragmentation of formerly continuous marsh area into discontinuous patches has been identified as contributing to reduced abundances of fishes and crustaceans in first-order creeks in other areas in the western Atlantic (Valentine-Rose et al. 2007; Lowe and Peterson 2014); this anthropogenic change is more likely to affect smaller, less mobile organisms such as cyprinodont fishes (Lowe and Peterson 2014; this study). Habitat connectivity appears to be a factor influencing residency and movement of *Fundulus heteroclitus* in salt marsh seascapes (Rozas et al. 1988; Able et al. 2012).

Related to the presence/absence of contiguous marsh, culverts were also in best-fitting throw trap BIOENV models. These structures can act as barriers to animal movement in salt marsh creeks (Stevens et al. 2006; Eberhardt et al. 2011) and fragment formerly continuous marsh habitat (Kennish 2001). In North Carolina, culverts are considered an anthropogenic factor compromising the quality of estuarine fish habitat (Deaton et al. 2006). Culverts may impede downstream movement of resident fishes or upstream movement of transient estuarine predators, effectively trapping fish biomass above them (Stevens et al. 2006). One creek with a short culvert (Atlantic Veneer) had catch rates of both small and large *Fundulus heteroclitus* that were higher than the two study creeks without culverts (Porters and Webb Creeks). Thus, the impact of culverts on resident species remains unclear. Sampling logistics restricted our throw trap sampling to only one creek that lacked a culvert (Porters Creek). We elected not to include culvert presence/absence as a categorical factor in

follow-up models because it did not separate creek communities as strongly as the presence/lack of marsh connectivity and there was only one creek where we throw trapped that lacked a culvert.

Water depth also appears to be an important determinant of nekton abundances in tidal creeks (Allen et al. 2007). This geomorphological metric was associated with community differences in throw trap samples. The dominant fish in our study, *Fundulus heteroclitus*, prefers shallow, largely intertidal creeks (Ruiz et al. 1993; Smith and Able 1994; Bretsch and Allen 2006; Allen et al. 2007; Meyer and Posey 2009). Our shallow study sites included Atlantic Veneer, Porters, Pelletier West, and Spooners Creeks, which had high or moderate abundances of *Fundulus heteroclitus*. Atlantic Veneer, the creek with the shallowest mean channel depth, consistently had the greatest catch of minnow trapped *Fundulus heteroclitus*. In contrast, we found minnow trapped *Lagodon rhomboides* to be most abundant in creeks with greater mean channel depths (Pelletier East and Webb Creeks), which is consistent with previous observations that this species prefers deeper waters than marsh residents such as *Fundulus heteroclitus* (Bretsch and Allen 2006; Meyer and Posey 2009).

Visually estimated stem density of *Spartina alterniflora* is a possible explanation for differences in abundances of resident nekton among study creeks. This habitat factor was not considered as a factor in throw trap BIOENV analyses because it was incorporated into estimates of catchability for dominant taxa collected by this gear type. For amphipods that attach themselves to stems of emergent marsh vegetation (Covi and Kneib 1995), this could explain higher densities of this taxon in Pelletier East and Pelletier West Creeks. However, it would not simultaneously explain lower densities of *Fundulus heteroclitus* from these creeks;

while *Fundulus heteroclitus* is a species that relies heavily on *Spartina alterniflora* for refuge (Kneib 1986), it was found in greater densities in creeks with the lowest stem density of *Spartina alterniflora*. Amphipods may respond to vegetation density on more localized scales than *Fundulus heteroclitus* or it may be that *Fundulus heteroclitus* prefers lower stem densities.

Contrasting patterns of abundance between *Fundulus heteroclitus* and one of its prey types (amphipods) suggest that, in addition to habitat or environmental factors, predator-prey interactions may influence densities of nekton in small saltwater creeks (Bass et al. 2001). Amphipods, the most abundant species in throw trap samples, are common prey of both adult and juvenile *Fundulus heteroclitus* (Nixon and Oviatt 1973; Kneib 1986; Allen et al. 1994) and were at their lowest densities in creeks with the highest *Fundulus heteroclitus* abundances. Predator-prey dynamics may also explain why the abundance of another prey of adult *Fundulus heteroclitus* (Kneib 1986), *Palaemonetes* spp., did not directly relate to creek alteration levels despite previous research showing that this taxa is more abundant in creeks with less development, more extensive *Spartina alterniflora* marsh, and lower percentages of armored shoreline (Fulton et al. 1996; Porter et al. 1997; Key et al. 2006; Krebs et al. 2014b).

Researchers have found the amount of marsh edge to be a determinant of nekton abundance in salt marsh creeks (Baltz et al. 1993; Minello et al. 1994; Peterson and Turner 1994; Kneib 2003; Visintainer et al. 2006). As an interface between two different habitat types, edge represents access to the marsh by nekton and its value to these species is often evaluated by examining the ratio of linear edge to vegetated marsh area in a system (Boström et al. 2011). The ratio of edge to vegetated habitat area is greater for small habitat patches than large ones (Wiens et al. 1993). In our creeks, the ratio of edge to area was predictably

negatively correlated with proportional marsh area (Spearman $r = -0.90$, $p = 0.005$). Thus, proportional marsh area in a creek represented both the edge and areal vegetation effects. Creeks such as Porters and Pelletier East, with relatively low amounts of proportional marsh area, had relatively high proportional edge compared to the other three marsh creeks that were sampled. This may offer an explanation for the continued production of some estuarine species in altered coastal habitats (Chesney et al. 2000) and, in our study, for the close association of the decapod *Callinectes sapidus* with the sparsely vegetated- and highly altered Pelletier East Creek. Our throw trap sampling in this creek was restricted to a laterally narrow swath of salt marsh there. *Callinectes sapidus* tends to be more abundant near edges (Peterson and Turner 1994; Minello 1999) and also forages more successfully in these spaces (Lewis and Eby 2002). *Lagodon rhomboides*, *Mugil* spp. and xanthid crabs also appear to prefer marsh edge (Peterson and Turner 1994), and were closely associated with Pelletier East in the 2013 throw trap ordination.

For the smaller fish caught in throw traps, two cyprinodonts, *Gambusia holbrooki* and *Cyprinodon variegatus*, were more closely associated with creeks with more altered characteristics such as high watershed imperviousness, culverts, and discontinuous marsh downstream. This was also seen for larger-sized *Gambusia holbrooki* and *Cyprinodon variegatus* in minnow traps (Figure 2.7; Table 2.6) but these two species were not in the best-fitting minnow trap BIOENV model in either year. *Gambusia holbrooki* is found in lower densities at higher salinities (Alcaraz and Garcia-Berthou 2007) and appears to optimize individual growth in marsh habitats that receive artificial freshwater pulses (Piazza and LaPeyre 2010); this would explain why this species associated most closely with Pelletier West, the creek with the greatest imperviousness and lowest salinity. *Cyprinodon variegatus*

utilizes *Spartina alterniflora* marshes for habitat (Peterson and Turner 1994; Rozas and Zimmerman 2000). However, as was the case in this study, *Cyprinodon variegatus* has been found in disturbed creeks in Gulf of Mexico estuaries (Lowe and Peterson 2014), potentially due to its ability to withstand highly variable water quality (Nordlie 1985) or due to a release from competition with *Fundulus* spp. (Lowe and Peterson 2014). Additionally, *Gambusia holbrooki*, *Cyprinodon variegatus* and *Lagodon rhomboides* were found in greater abundances in creeks possessing standing water than those lacking it.

Transient species were relatively rare in our study. *Lagodon rhomboides*, an omnivorous fish (Muncy 1984) and the only transient taxon caught in abundance by either gear, associated most closely with deeper creeks that possessed little or no marsh surface and had alterations at the creek- (low percentages of marsh, shoreline armoring) and watershed levels (high imperviousness). Lowe and Peterson (2014) found *Lagodon rhomboides* to be more abundant in urbanized tidal creeks along the U.S. Gulf of Mexico coastline and described this species as being able to exploit altered estuarine habitats. The high abundance of *Lagodon rhomboides* in non-vegetated Webb Creek does not support the previous assertion that marsh habitat is a critical nursery area for this species (Shervette and Gelwick 2007). Differences in recruitment levels among creeks appear to be an unlikely explanation for differences in catch rates of this transient species, given that creeks differing markedly in catch rates were in geographically close proximity.

Recovery efficiency of the throw trap varied among taxa. We adjusted the catch so that the community analyses were not biased to fauna with high recovery efficiencies. Rozas and Minello (1997) reviewed throw trap catch efficiencies (a combination of gear capture efficiency and recovery efficiency) and found them to be high and invariant by habitat type.

We also found recovery efficiency to be high but influenced by water depth and vegetation stem density. Given that estimated absolute densities (corrected for recovery efficiency) were roughly 25 and 35 percent higher than the cumulative catch for two species, we suggest that future research using enclosure-type sampling devices (e.g., throw traps) within marsh or other heterogeneous habitats employ these or similar methods to estimate recovery efficiencies for main species and habitat types.

It is important to point out that the method we used to estimate absolute abundances addresses a bias in failing to collect the full number of fauna enclosed by the throw trap (recovery efficiency) but does not address gear ‘capture efficiency’ (Rozas and Minello 1997). This is one reason why we sampled with two different gear types in this study.

Initiatives to maintain the biological integrity of developing watersheds require understanding the relationship between metrics of urbanization and biological integrity (Wang et al. 1997). Studies into the status and trends of biological production become more difficult the further estuarine habitats become altered from baseline conditions (Peterson and Lowe 2009). While each creek had a unique suite of habitat and anthropogenic characteristics, we recognize that, across study sites, some factors were correlated or were not replicated. Increasing the number of study sites and then conducting similar analyses would further elucidate the influence of specific habitat and urbanization factors, and combinations of factors, on biological communities in tidal creeks in this region.

Coastal development will continue to place anthropogenic stress on *Spartina alterniflora* salt marsh creeks, which are vital to fish and crustacean production in the U.S. Atlantic coastal plain. Roughly 12% of salt marsh habitats in the U.S. South Atlantic region have been lost to development (Gedan and Silliman 2009) and the watersheds of creeks

sampled for this study are forecast to continue increasing in human population. Our findings in the southeast U.S. can be viewed as the minimum human impact that can be anticipated if the forecasted coastal development to this geographic area continues. Our results predict that densities of dominant resident salt marsh nekton, such as *Fundulus heteroclitus* and *Palaemonetes* spp., are likely to decline and densities of habitat generalist species, such as *Lagodon rhomboides*, are likely to increase with the loss of marsh and continued conversion of upland from vegetated to impervious surfaces. Agencies charged with permitting coastal development should consider the impacts to nekton communities from development projects that reduce marsh area and sever the connectivity between marshes patches across the U.S. South Atlantic coastal landscape.

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Table 2.1. Habitat and environmental characteristics for six tidal creeks in coastal North Carolina sampled for nekton communities with a 1 m² throw trap and wire mesh minnow traps monthly from spring-fall 2012 and 2013. Metrics apply only to that portion of each creek over which gears were set (see *Methods*). Minnow trap sampling was conducted in all six creeks; throw trap sampling was conducted in each creek except Webb Creek. Measurements with associated parenthesis are: mean (standard error).

Creek metric / Sample gear	Measurement	Atlantic Veneer	Porters	Pelletier East	Pelletier West	Spooners	Webb
Watershed area (m ²)		414,224	1,095,729	1,127,387	698,413	490,859	86,951
Impervious area (m ²)		64,322	110,166	260,740	325,629	64,220	20,074
Vegetated edge (m)		500	1,200	145	500	400	0
Watershed impervious %		15.5	10.0	23.1	46.7	13.0	23.1
High tide wetted area (m ²)		5,209	15,162	4,170	5,427	7,691	13,494
Marsh area (m ²)		4,247	9,498	112	3,707	6,324	0
High tide marsh area (%)		81.5	62.6	2.7	68.3	82.2	0
Culvert downstream?		Yes	No	Yes	Yes	Yes	No
Marsh downstream?		Yes	Yes	No	No	Yes	No
Standing water at low tide		No	No	Yes	Yes	No	Yes
Throw trap	Creek channel depth (m), mean	0.21	0.27	0.96	0.28	0.29	2.00
	Distance from channel (m), mean	5.8 (0.1)	11.25 (0.9)	0.4 (0.1)	4.7 (0.3)	3.5 (0.5)	-
	Distance from channel (m), range	0 - 27	0 - 45	0 - 2	0 - 17	0 - 40	-
	Depth (m), mean	0.19 (0.01)	0.23 (0.01)	0.19 (0.01)	0.19 (0.01)	0.19 (0.01)	-
	Depth (m), range	0.1 - 0.5	0.1 - 0.6	0.1 - 0.5	0.1 - 0.5	0.1 - 0.6	-
	Temperature (°C), mean	24.9 (0.4)	26.0 (0.4)	27.6 (0.4)	26.8 (0.4)	27.3 (0.5)	-
	Temperature (°C), range	15.1 - 34.7	17.1 - 37.5	21.1 - 33.4	15.8 - 34.9	18.7 - 35.9	-
	Salinity (psu), mean	30.0 (0.7)	25.8 (0.5)	21.0 (0.9)	17.6 (0.8)	25.6 (1.0)	-
	Salinity (psu), range	5 - 39	4 - 35	6 - 35	0 - 30	3 - 40	-
	Dissolved oxygen (mg/l), mean	4.83 (0.12)	5.26 (0.20)	5.7 (0.3)	5.0 (0.27)	4.2 (0.2)	-
Minnow trap	Dissolved oxygen (mg/l), range	2.28 - 8.17	1.90 - 11.06	1.67 - 14.20	1.28 - 12.20	1.71 - 8.99	-
	Temperature (°C), mean	24.8 (0.5)	25.3 (0.4)	27.5 (0.4)	25.0 (0.4)	26.2 (0.5)	26.2 (0.4)
	Temperature (°C), range	13.3 - 35.3	13.5 - 37.5	16.1 - 32.7	13.6 - 34.5	8.3 - 36.1	18.7 - 31.8
	Salinity (psu), mean	26.9 (0.8)	27.5 (0.5)	18.4 (0.9)	17.8 (0.8)	20.7 (0.9)	28.9 (0.3)
	Salinity (psu), range	10 - 40	5 - 35	0 - 35	0 - 31	0 - 39	22 - 34
	Dissolved oxygen (mg/l), mean	4.28 (0.13)	5.53 (0.15)	5.85 (0.25)	5.25 (0.25)	4.65 (0.13)	5.63 (0.20)
	Dissolved oxygen (mg/l), range	2.02 - 8.17	2.14 - 11.00	2.62 - 14.20	1.58 - 12.04	2.41 - 9.45	2.23 - 8.66

Table 2.2. Number (n) and percent frequency (%) of each fish and invertebrate taxa captured by a 1 m² throw trap actively deployed on the marsh surface (n = 640 deployments) in five tidal creeks in coastal North Carolina from spring through fall of 2012 and 2013. Taxa in bold are those for which catch data were analyzed with non-metric multidimensional scaling.

Year	2012		2013	
Species	n	%	n	%
<i>Amphipoda</i>	4,250	61.55	3,547	57.37
<i>Fundulus heteroclitus</i>	1,065	15.42	1,004	16.24
<i>Palaemonetes</i> spp.	791	11.46	602	9.74
<i>Gambusia holbrooki</i>	581	8.41	579	9.36
<i>Cyprinodon variegatus</i>	102	1.48	84	1.36
<i>Xanthidae</i>	4	0.06	169	2.73
<i>Farfantepenaeus</i> spp.	16	0.23	89	1.44
<i>Callinectes sapidus</i>	25	0.36	20	0.32
<i>Fundulus diaphanus</i>	19	0.28	22	0.36
<i>Dormitator maculatus</i>	16	0.23	20	0.32
<i>Mugil</i> spp.	22	0.32	11	0.18
<i>Menidia menidia</i>	8	0.12	12	0.19
<i>Lagodon rhomboides</i>	1	0.01	15	0.24
<i>Leiostomus xanthurus</i>	2	0.03	5	0.08
<i>Gobiosoma</i> spp.	2	0.03	1	0.02
<i>Anguilla rostrata</i>	-	-	2	0.03
<i>Eucinostomus argenteus</i>	-	-	1	0.02
<i>Centropomus undecimalis</i>	1	0.01	-	-

Table 2.3. Number of trap sets and individuals of each taxon captured by a 1 m² throw trap actively deployed on the marsh surface in five tidal creeks in coastal North Carolina from spring through fall of 2012 and 2013.

Creek	Atlantic Veneer		Porters		Pelletier East		Pelletier West		Spooners	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Number of traps set	70	70	70	70	44	39	70	70	67	70
<i>Amphipoda</i>	232	337	158	294	1602	642	977	1076	1281	1198
<i>Fundulus heteroclitus</i>	257	296	322	303	117	114	150	152	219	139
<i>Palaemonetes</i> spp.	122	156	344	181	273	215	7	1	45	49
<i>Gambusia holbrooki</i>	124	66	3	4	102	233	241	219	111	57
<i>Cyprinodon variegatus</i>	12	13			12	6	66	61	12	4
<i>Xanthidae</i>	1	54	3	88		4		7		16
<i>Farfantepenaeus</i> spp.			3	15	13	64		10		
<i>Callinectes sapidus</i>	3	1	9	12	8	6	2		3	1
<i>Fundulus diaphanus</i>	9	6	10	8				5		3
<i>Dormitator maculatus</i>		5			14	11			2	4
<i>Mugil</i> spp.	2	2	14	5	1	4	1		4	
<i>Menidia menidia</i>				2	8	10				
<i>Lagodon rhomboides</i>			1			15				
<i>Leiostomus xanthurus</i>			2	3		2				
<i>Gobiosoma</i> spp.	1		1			1				
<i>Anguilla rostrata</i>						1				1
<i>Eucinostomus argenteus</i>						1				
<i>Centropomus undecimalis</i>					1					

Table 2.4. Number (n) and percent frequency (%) of each fish and invertebrate taxa captured by 6.4 mm wire mesh minnow traps passively deployed (n = 1001 deployments) in non-vegetated channels of six tidal creeks in coastal North Carolina from spring through fall of 2012 and 2013. Taxa in bold are those for which catch data were analyzed with non-metric multidimensional scaling.

Year	2012		2013	
Species	n	%	n	%
<i>Fundulus heteroclitus</i>	14,915	87.24	14,355	93.00
<i>Lagodon rhomboides</i>	846	4.95	562	3.64
<i>Cyprinodon variegatus</i>	1,154	6.75	250	1.62
<i>Gambusia holbrooki</i>	119	0.70	175	1.13
<i>Gobiosoma</i> spp.	16	0.09	37	0.25
<i>Dormitator maculatus</i>	10	0.06	27	0.17
<i>Palaemonetes</i> spp.	10	0.06	4	0.03
<i>Fundulus diaphanus</i>	6	0.04	5	0.03
<i>Callinectes sapidus</i>	3	0.02	5	0.03
<i>Mugil</i> spp.	4	0.02	2	0.01
<i>Farfantepenaeus</i> spp.	3	0.02	3	0.02
<i>Leiostomus xanthurus</i>	1	<0.01	5	0.03
<i>Orthopristis chrysoptera</i>	5	0.03	-	-
<i>Anguilla rostrata</i>	1	<0.01	1	<0.01
<i>Lutjanus griseus</i>	-	-	1	<0.01
<i>Cynoscion nebulosus</i>	-	-	1	<0.01
<i>Eucinostomus argenteus</i>	1	<0.01	-	-
<i>Paralichthys lethostigma</i>	1	<0.01	-	-
<i>Bairdiella chrysoura</i>	1	<0.01	-	-
<i>Elops saurus</i>	-	-	1	<0.01
<i>Xanthidae</i>	-	-	1	<0.01

Table 2.5. Number of trap sets and individuals of each taxon captured by 6.4 mm wire mesh minnow traps passively deployed in non-vegetated channels of six tidal creeks in coastal North Carolina from spring through fall of 2012 and 2013.

Creek	Atlantic Veneer		Porters		Pelletier East		Pelletier West		Spooners		Webb	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Number of traps set	69	82	140	102	70	61	85	88	92	83	61	68
<i>Fundulus heteroclitus</i>	7831	6602	2369	1290	214	31	1464	2162	3037	4270		
<i>Lagodon rhomboides</i>			86	23	337	156	1	1	60	147	362	235
<i>Cyprinodon variegatus</i>	117	87	2	15	23	1	878	94	134	53		
<i>Gambusia holbrooki</i>	19	15	6		3	1	45	156	46	3		
<i>Gobiosoma</i> spp.	6	22	1	3		1	1		2	4	6	7
<i>Dormitator maculatus</i>	9	22	1			2		1		2		
<i>Palaemonetes</i> spp.			10	1		3						
<i>Fundulus diaphanus</i>	2		2	5					1			
<i>Callinectes sapidus</i>		2	2	1					1	2		
<i>Mugil</i> spp.	1	2							3			
<i>Farfantepenaeus</i> spp.		1	2	2	1							
<i>Leiostomus xanthurus</i>						1		3	1	1		
<i>Orthopristis chrysoptera</i>											5	
<i>Anguilla rostrata</i>				1					1			
<i>Lutjanus griseus</i>												1
<i>Cynoscion nebulosus</i>										1		
<i>Eucinostomus argenteus</i>	1											
<i>Paralichthys lethostigma</i>					1							
<i>Bairdiella chrysoura</i>			1									
<i>Elops saurus</i>									1			
<i>Xanthidae</i>												1

Table 2.6. Annual mean (\pm standard deviation (S.D.)) and range of total lengths (TL: mm) of the fish species *Fundulus heteroclitus*, *Gambusia holbrooki*, and *Cyprinodon variegatus* captured by a 1 m² throw trap and wire mesh minnow traps fished in North Carolina tidal creeks in 2012 and 2013.

Species	Gear	Year	Mean TL (\pm S.D.)	Range TL
<i>Fundulus heteroclitus</i>	Throw trap	2012	26.8 (13.6)	2.5 – 91.0
		2013	23.0 (15.0)	3.4 – 92.0
	Minnow trap	2012	57.7 (12.1)	28.0 – 103.0
		2013	58.6 (10.8)	27.0 – 110.0
<i>Gambusia holbrooki</i>	Throw trap	2012	22.4 (9.3)	4.2 – 48.0
		2013	21.8 (10.5)	3.6 – 48.0
	Minnow trap	2012	41.6 (2.9)	35.0 – 50.0
		2013	41.8 (2.9)	31.0 – 47.0
<i>Cyprinodon variegatus</i>	Throw trap	2012	37.9 (13.2)	5.9 – 60.0
		2013	33.7 (14.7)	6.1 – 62.0
	Minnow trap	2012	46.6 (6.3)	27.0 – 64.0
		2013	49.4 (5.5)	34.0 – 61.0

Table 2.7. Results of fitting normally distributed general linear models to cumulative recovery efficiency ($q_{deployment}$) of four resident salt marsh taxa by a 1 m² throw trap. Covariates of $q_{deployment}$ considered in each model set included water depth (depth), percent *Spartina alterniflora* stem coverage in each trap (*Spartina*), and the interaction between these factors. AIC = Akaike Information Criteria (AIC). The ΔAIC value for each model was calculated as the difference between the value of any particular model (AIC_i) and the minimum AIC (best fitting model) in each taxon-specific model set. Number of model parameters = k. Akaike weight = w_i . Intercepts and regression coefficients are listed in parentheses for the best fitting model in each model set.

Species/Taxon	Model	k	AIC	ΔAIC	w_i
<i>Fundulus heteroclitus</i>	(1.084) <i>Spartina</i> (-0.003)	2	-11.02	0	0.42
	Null	1	-10.03	0.99	0.25
	Depth + <i>Spartina</i>	3	-9.08	1.94	0.16
	Depth	2	-8.37	2.65	0.11
	Depth + <i>Spartina</i> + Depth* <i>Spartina</i>	4	-7.12	3.90	0.06
	<i>Gambusia holbrooki</i>	Null (0.975)	1	-52.80	0
Depth		2	-51.07	1.73	0.18
<i>Spartina</i>		2	-50.92	1.88	0.16
Depth + <i>Spartina</i> + Depth* <i>Spartina</i>		4	-50.88	1.92	0.16
Depth + <i>Spartina</i>		3	-49.31	3.49	0.07
<i>Palaemonetes</i> spp.	(1.304) Depth (-1.221)	2	5.77	0	0.54
	Depth + <i>Spartina</i>	3	7.77	1.92	0.20
	Depth + <i>Spartina</i> + Depth* <i>Spartina</i>	4	8.89	3.84	0.11
	Null	1	9.47	6.55	0.09
	<i>Spartina</i>	2	10.19	7.32	0.06
Amphipoda	Null (0.821)	1	-3.37	0	0.33
	<i>Spartina</i>	2	-2.86	0.51	0.26
	Depth + <i>Spartina</i>	3	-2.37	1.00	0.20
	Depth	2	-1.49	1.88	0.13
	Depth + <i>Spartina</i> + Depth* <i>Spartina</i>	4	-0.38	2.99	0.07

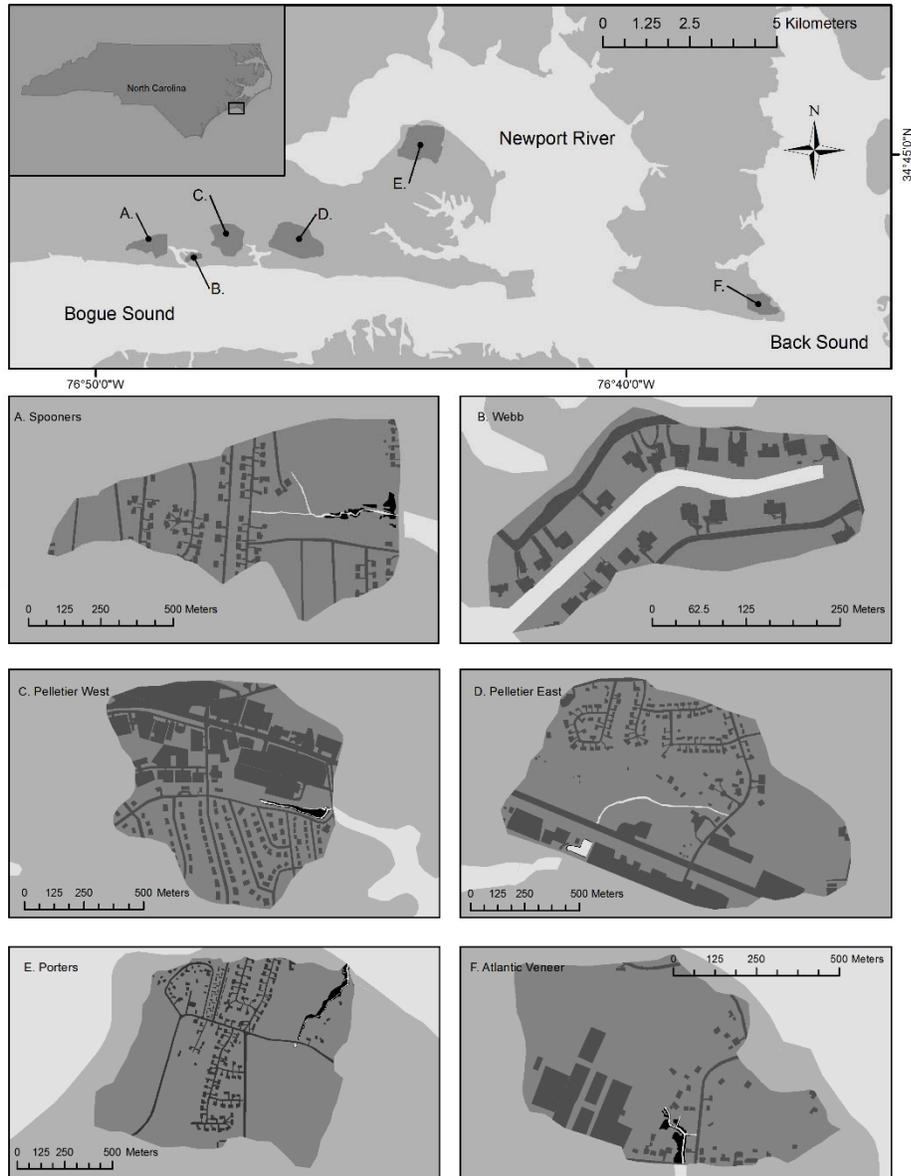


Figure 2.1. Map of six tidal creeks in coastal North Carolina sampled with a 1 m² throw trap and 6.4 mm wire mesh minnow traps used to estimate densities and relative abundances of epibenthic fishes and crustaceans from spring through fall of 2012 and 2013. Darker shading on the larger inset map represents the watershed of each creek; this is also the shade showing the watersheds in each creek-specific map. The darkest gray shade for each creek map represents hardened (impervious) surface. The off-white and black in each creek map are the areas of the creek channel and marsh surface, respectively. Minnow trapping was conducted in all six creeks. Throw trapping was conducted in all creeks except Webb Creek.

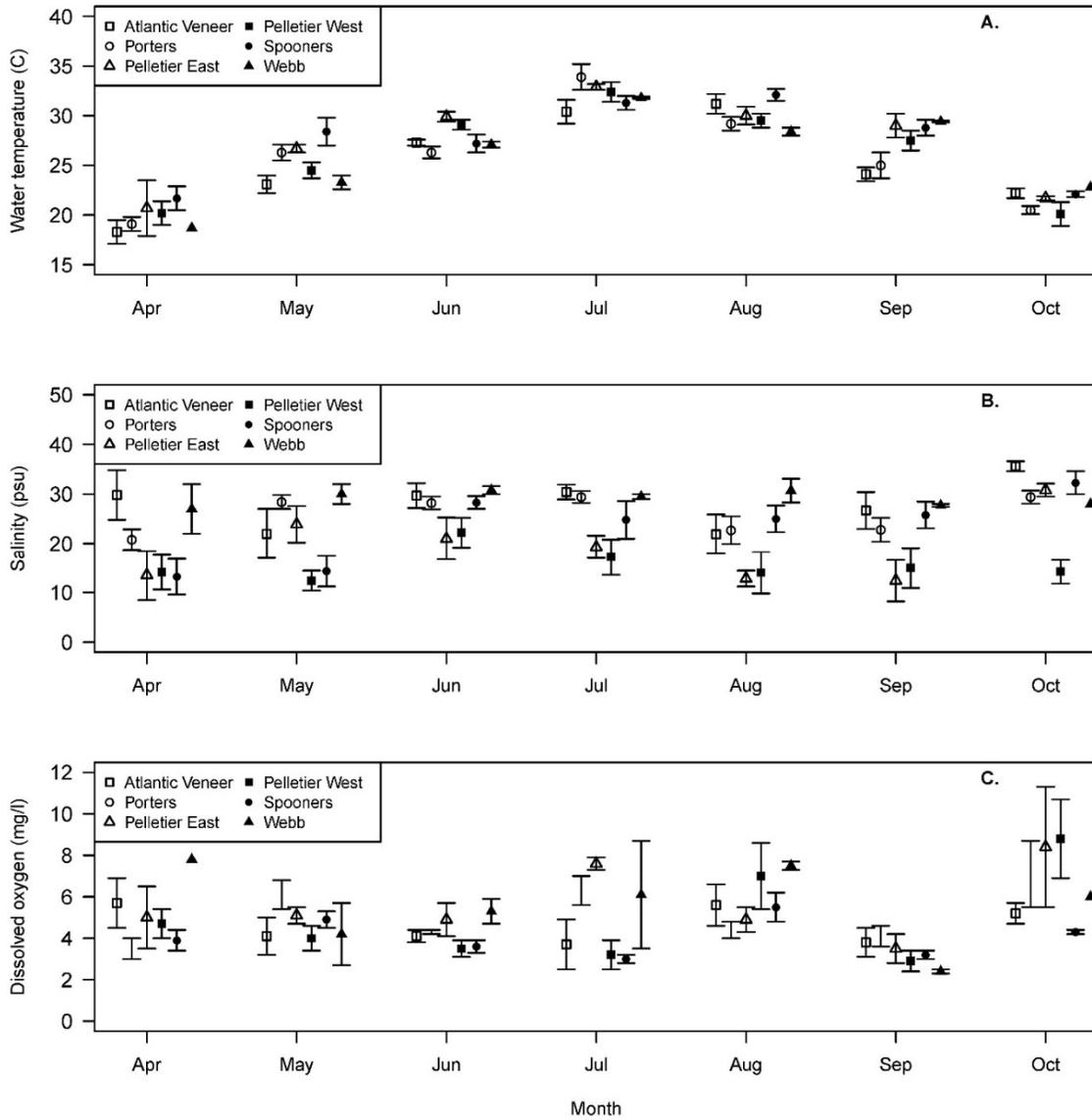


Figure 2.2. Mean (\pm S.E.) monthly water temperature ($^{\circ}$ C) (panel A), salinity (psu) (panel B), and dissolved oxygen concentration (mg/l) (panel C) in six tidal creeks in coastal North Carolina sampled from April through October of 2012 and 2013. Symbols for each creek are jittered around monthly tick marks to avoid overlap. Symbols without error bars were for creek/month combinations with only a single observation.

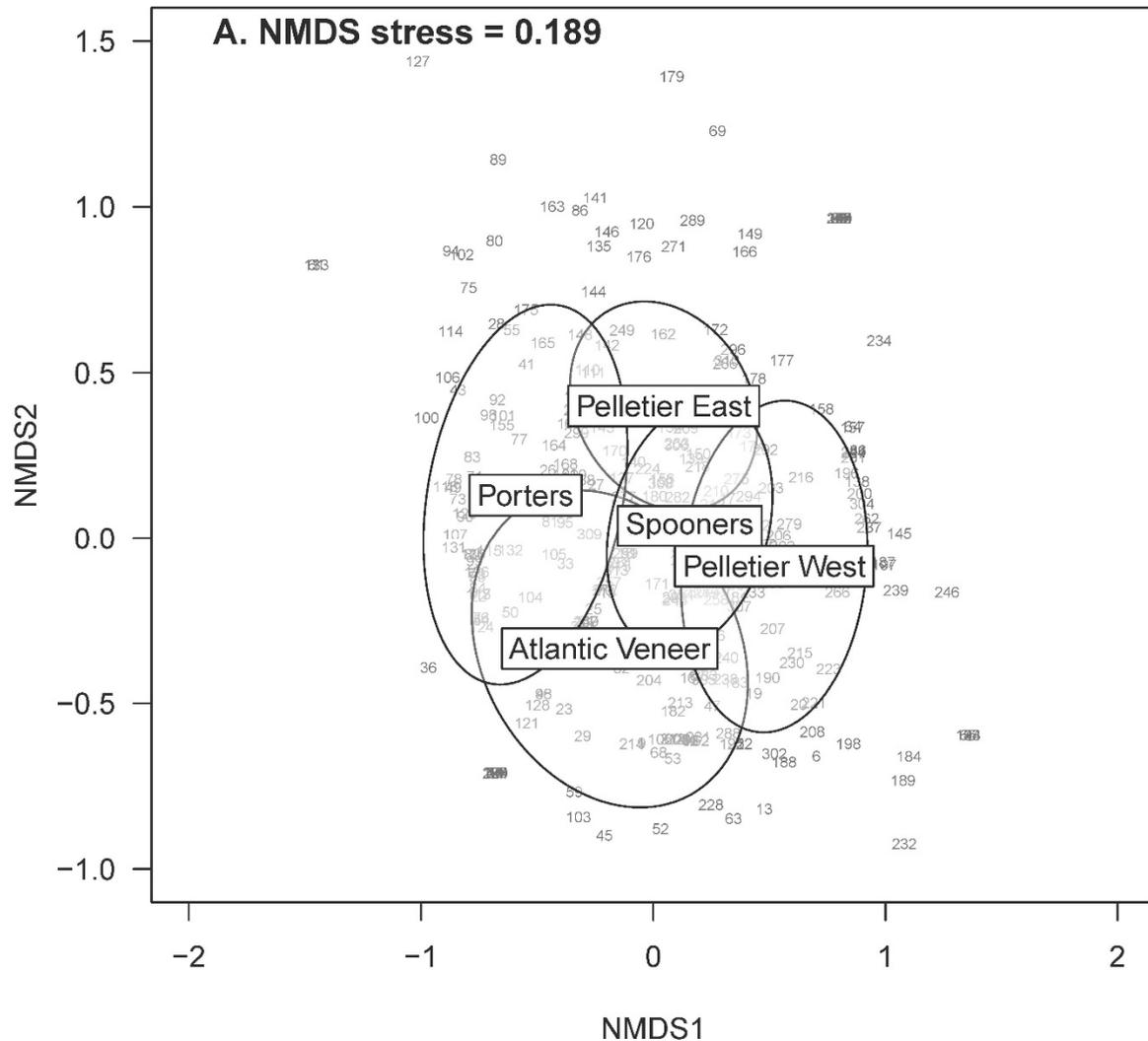


Figure 2.3. Non-metric multidimensional scaling ordination for 2012 throw trap samples from five salt marsh creeks showing (A) sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses; (B) the direction and strength of the group of fish and invertebrate densities that showed the greatest rank-correlation with sample dissimilarities, and (C) the centroid (location) of each class of binary environmental/habitat variables most rank-correlated with sample dissimilarities. Samples from each trap deployment are the small gray numbers. ‘Cul’= culvert; ‘MDn’ = marsh downstream of sample area. ‘C_sapidus’ in panel B is the species *Callinectes sapidus* and ‘Palaemonetes’ is the genus *Palaemonetes* spp. The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C).

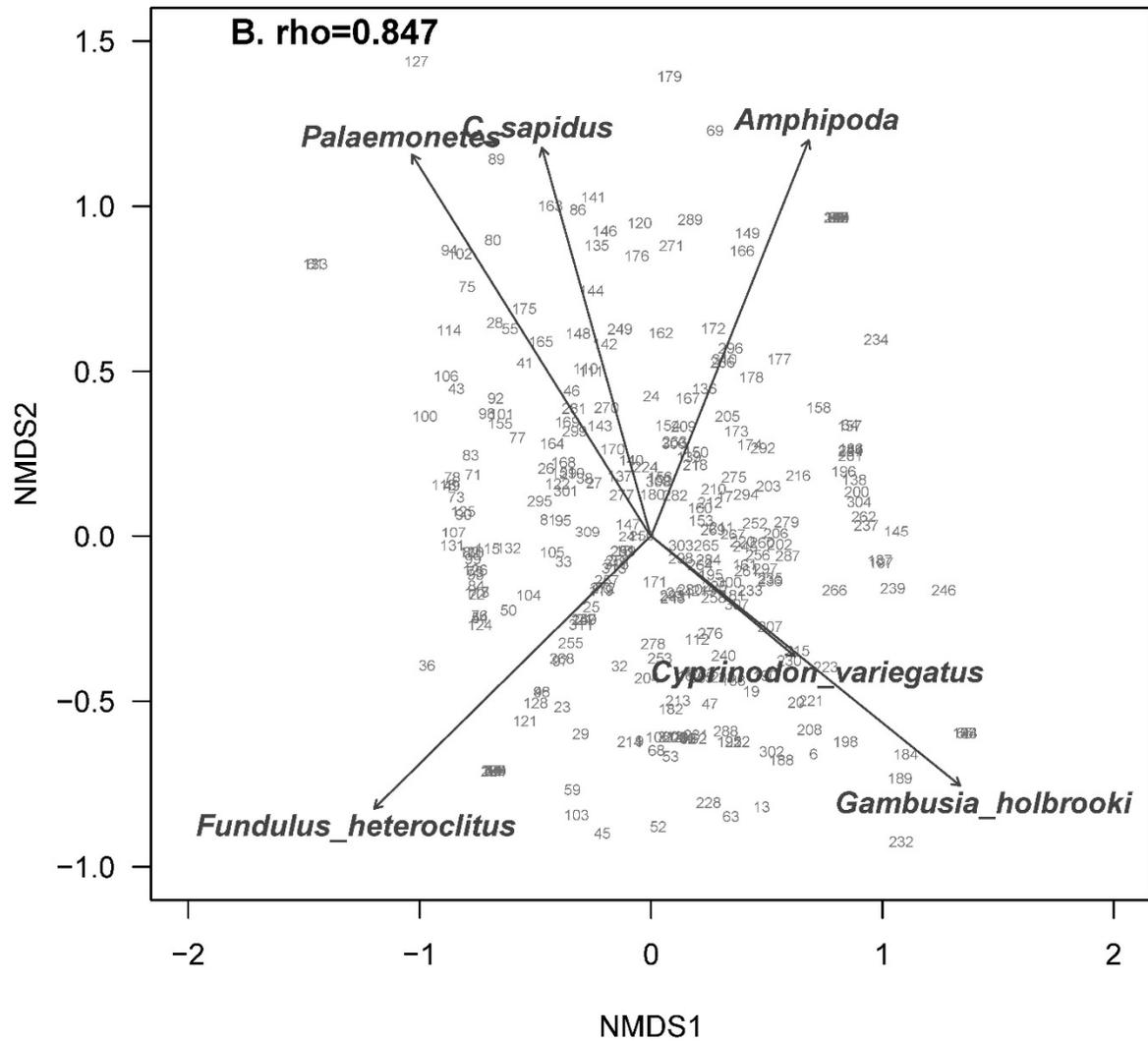


Figure 2.3 (con't)

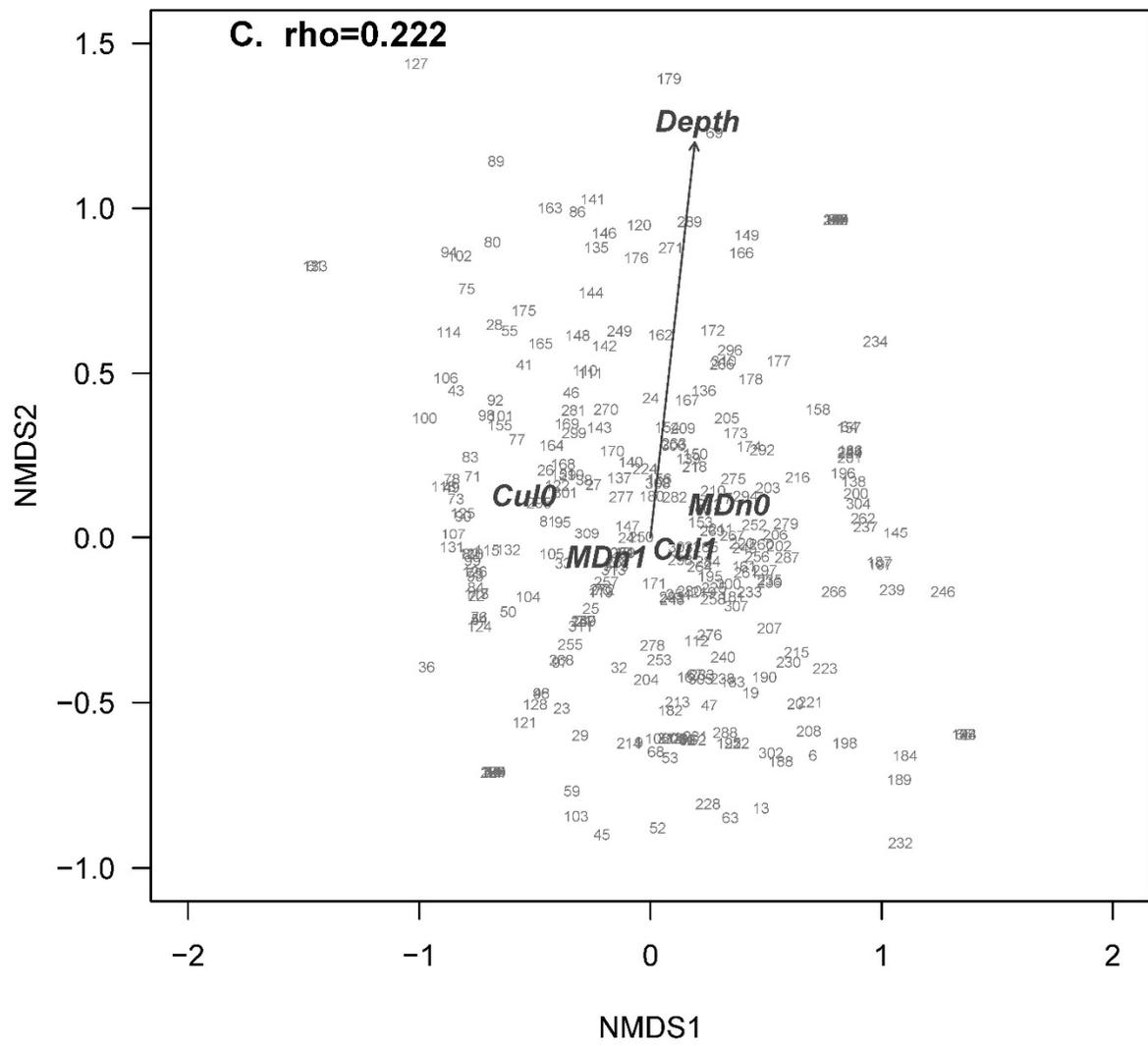


Figure 2.3 (con't)

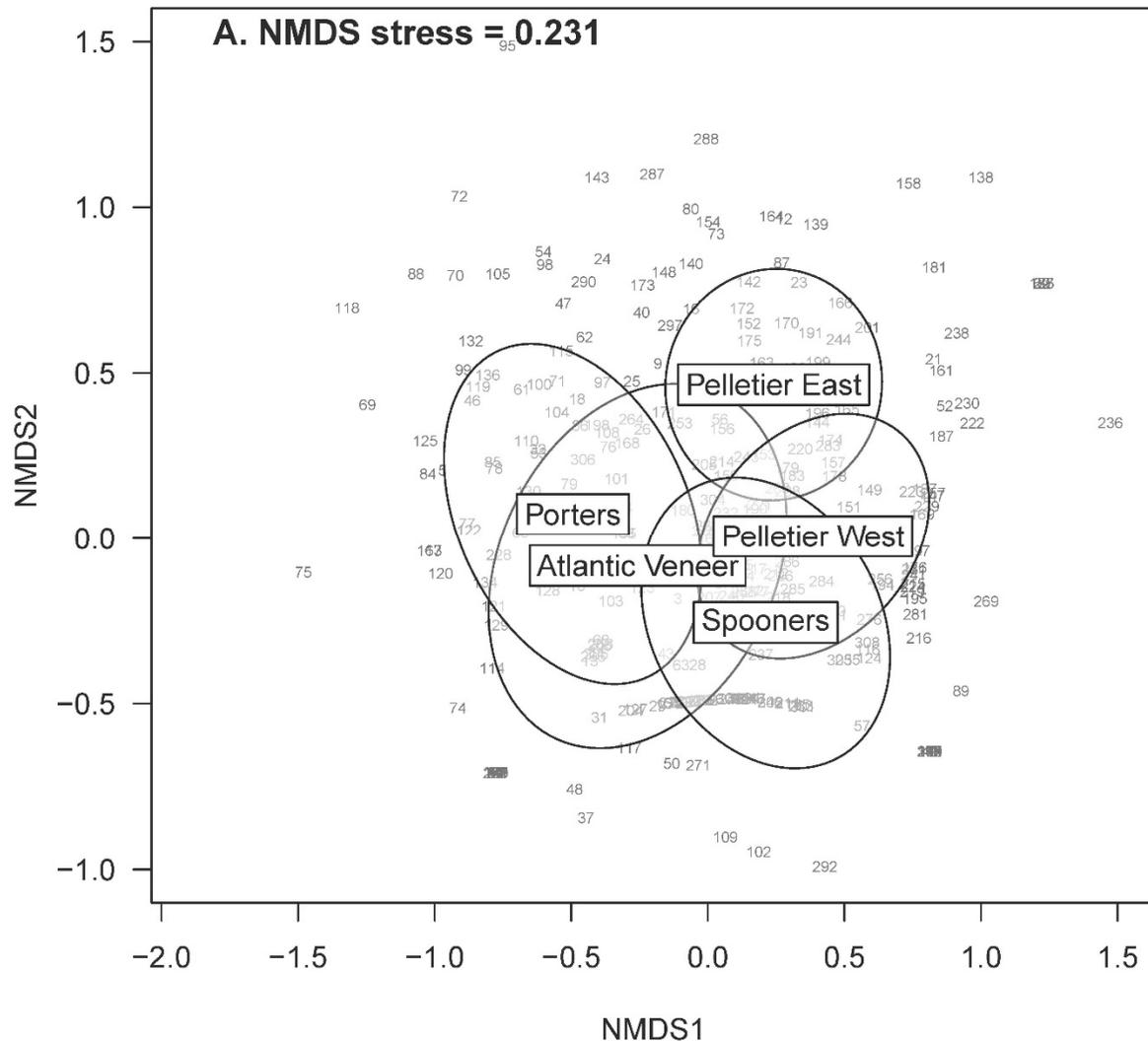


Figure 2.4. Non-metric multidimensional scaling ordination for 2013 throw trap samples from five salt marsh creeks showing (A) sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses; (B) the direction and strength of the group of fish and invertebrate densities that showed the greatest rank-correlation with sample dissimilarities; and (C) the direction and strength (length of the arrow) of continuous environmental/habitat variables, and the centroid (location) of each class of binary environmental/habitat variables most rank-correlated with sample dissimilarities. Samples from each trap deployment are the small gray numbers. ‘Cul’= culvert; ‘MDn’ = marsh downstream of sample area. The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C).

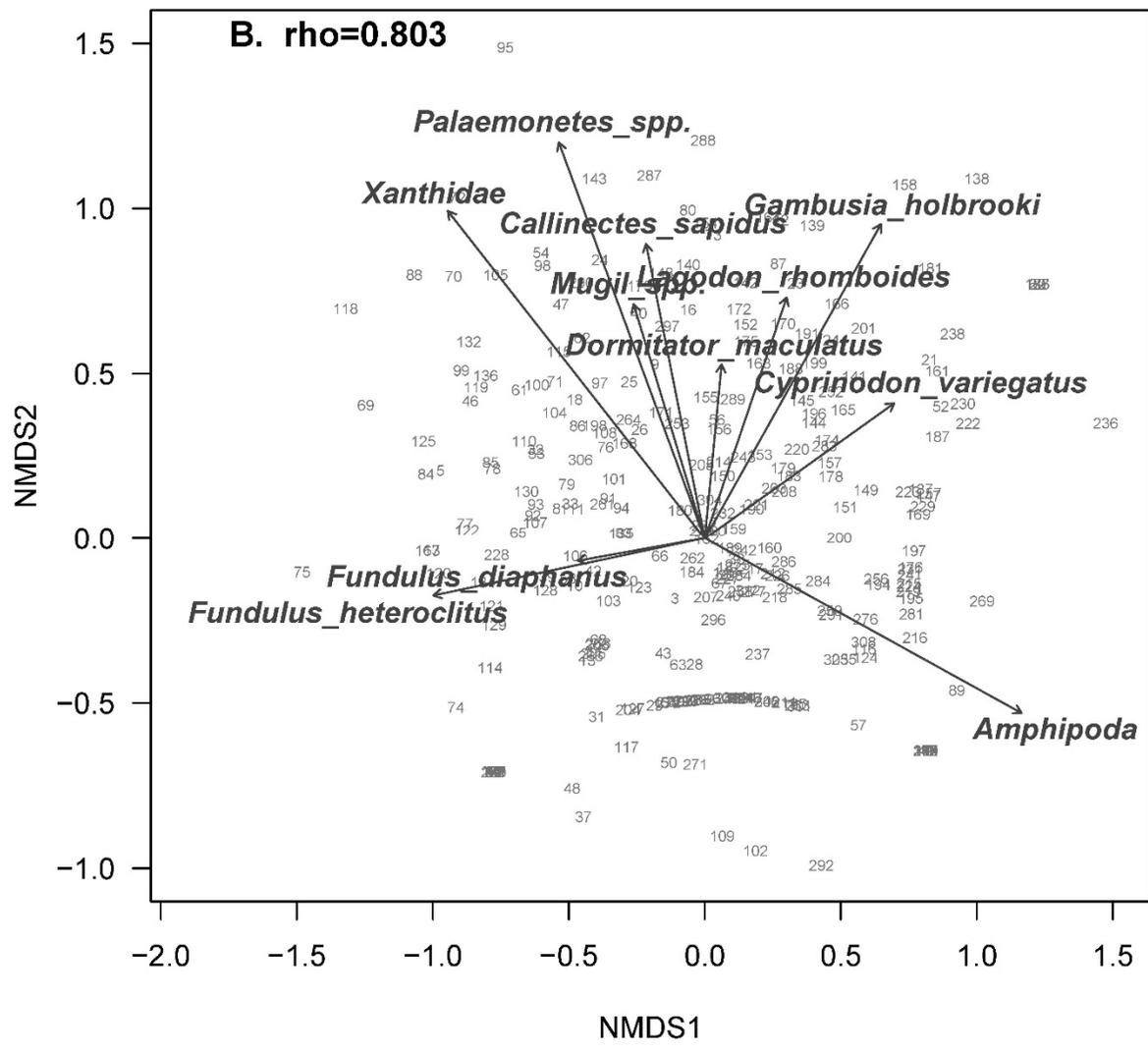


Figure 2.4 (con't)

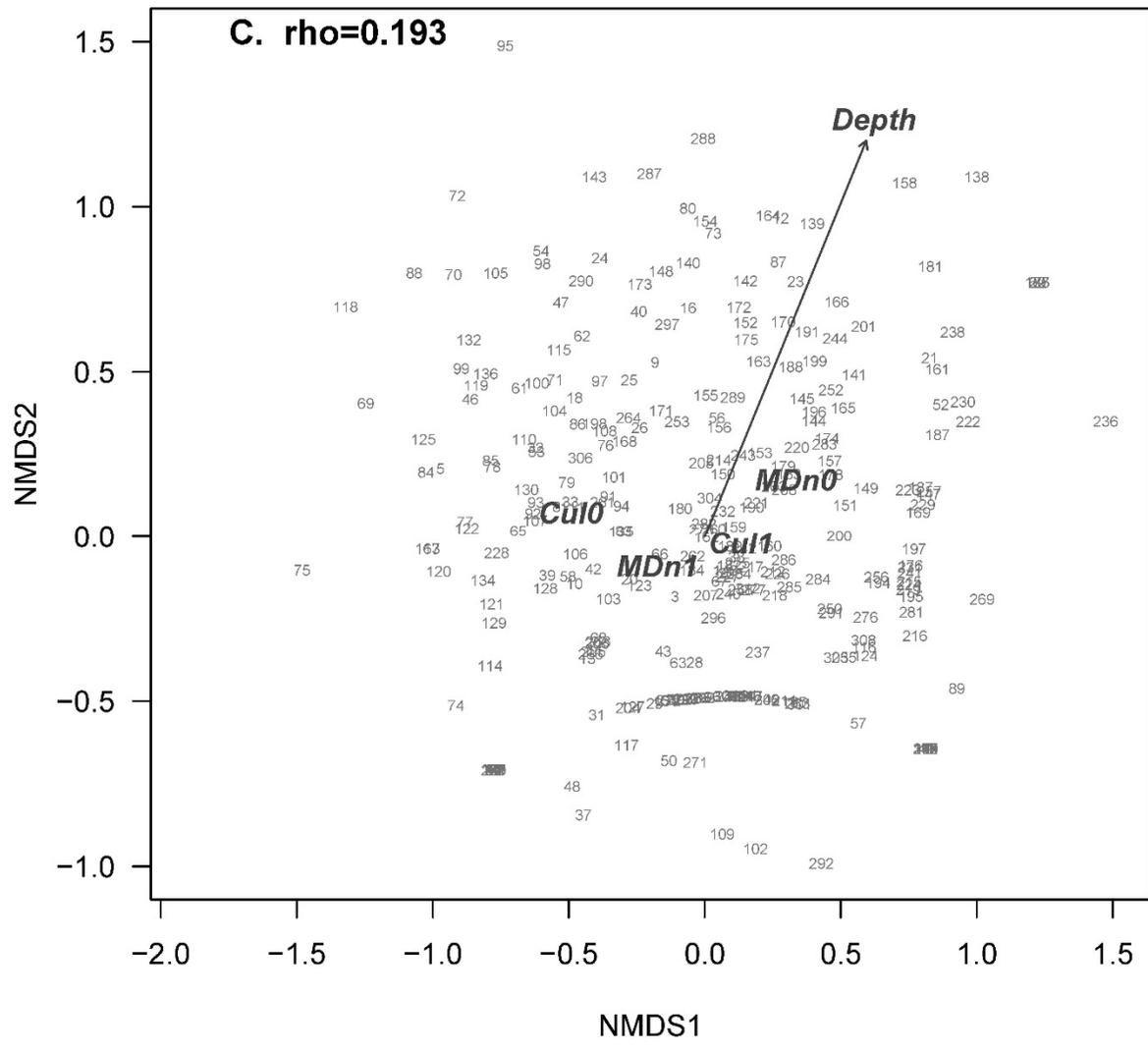


Figure 2.4 (con't)

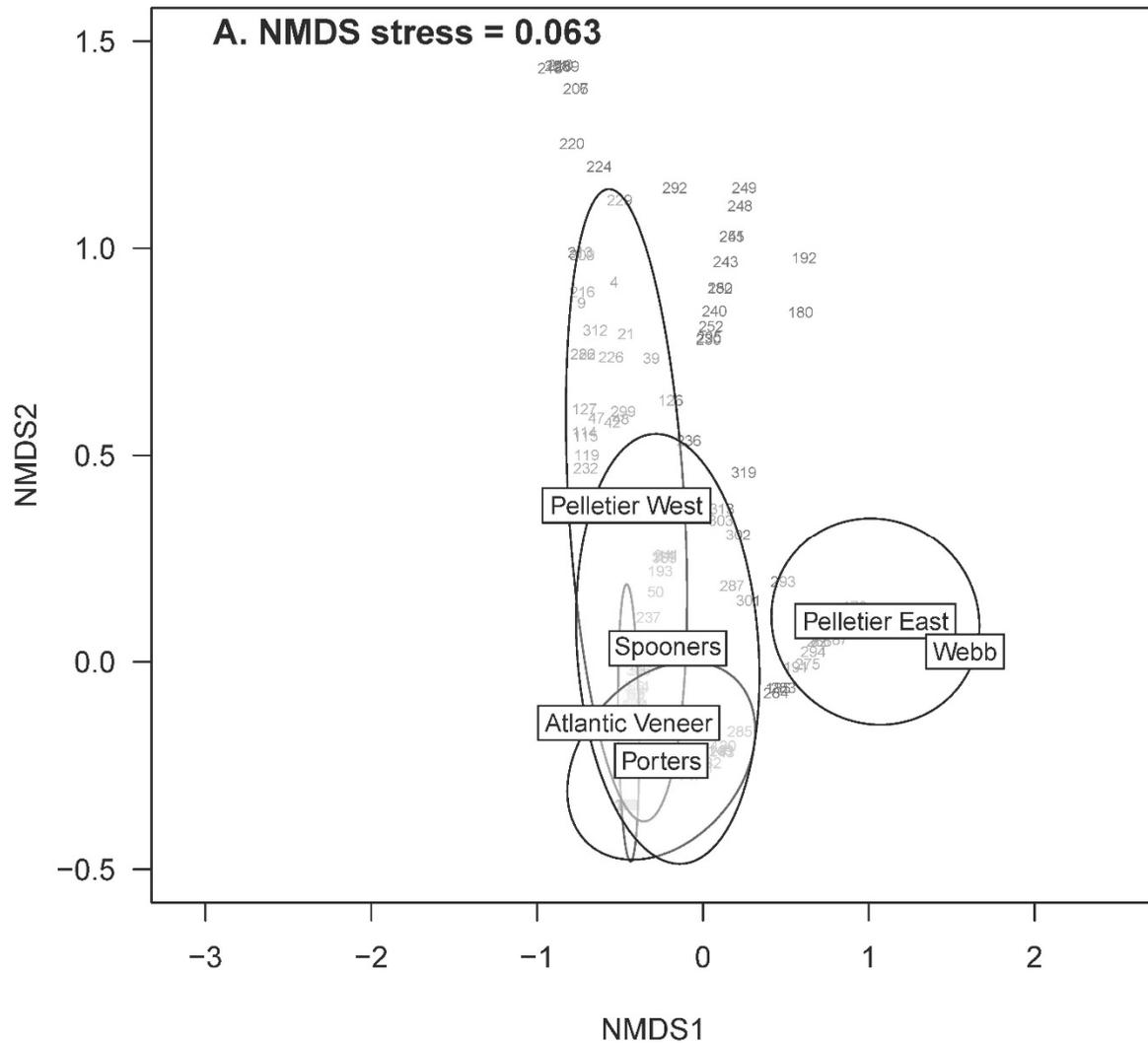


Figure 2.5. Non-metric multidimensional scaling ordination for 2012 minnow trap samples from six salt marsh creeks showing (A) sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses; (B) the direction and strength fish and invertebrate catches that showed the greatest rank-correlation with sample dissimilarities; and (C) the direction and strength (length of the arrow) of continuous environmental/habitat variables, and the centroid (location) of each class of binary environmental/habitat variables most rank-correlated with sample dissimilarities. Samples from each trap deployment are the small gray numbers. The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). ‘PctMarsh’ is percent of each creek’s high tide wetted area that is marsh.

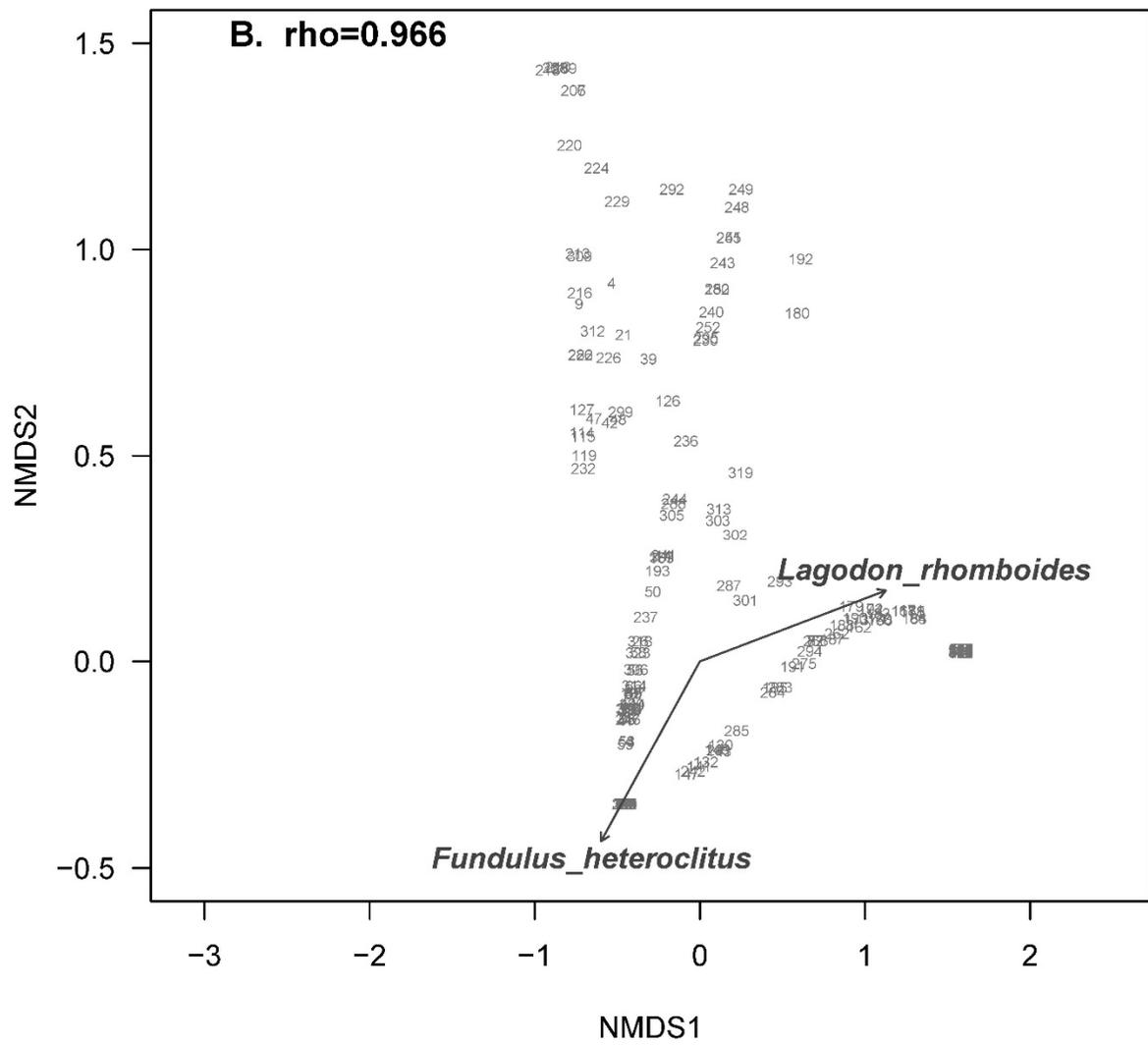


Figure 2.5 (con't)

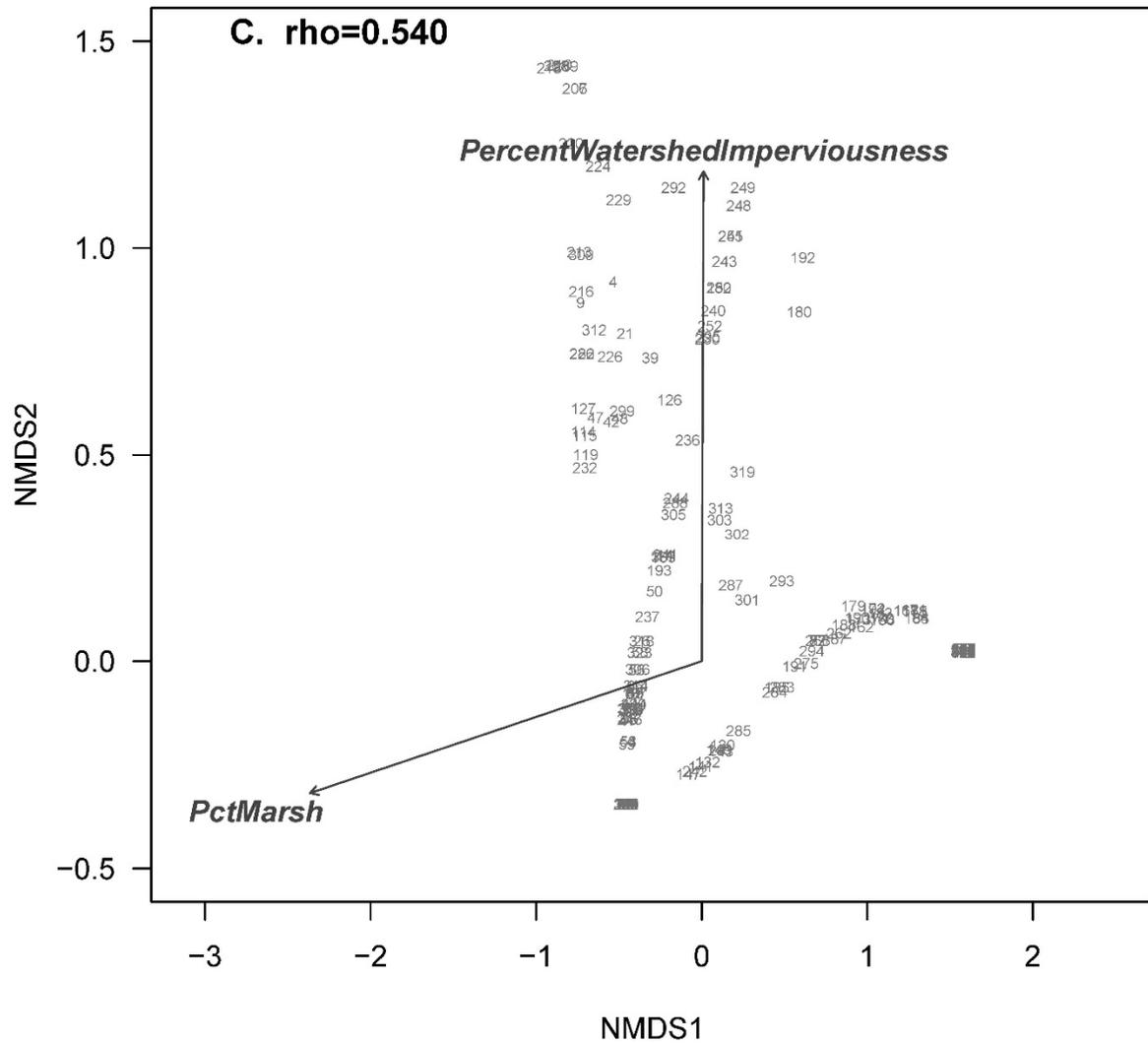


Figure 2.5 (con't)

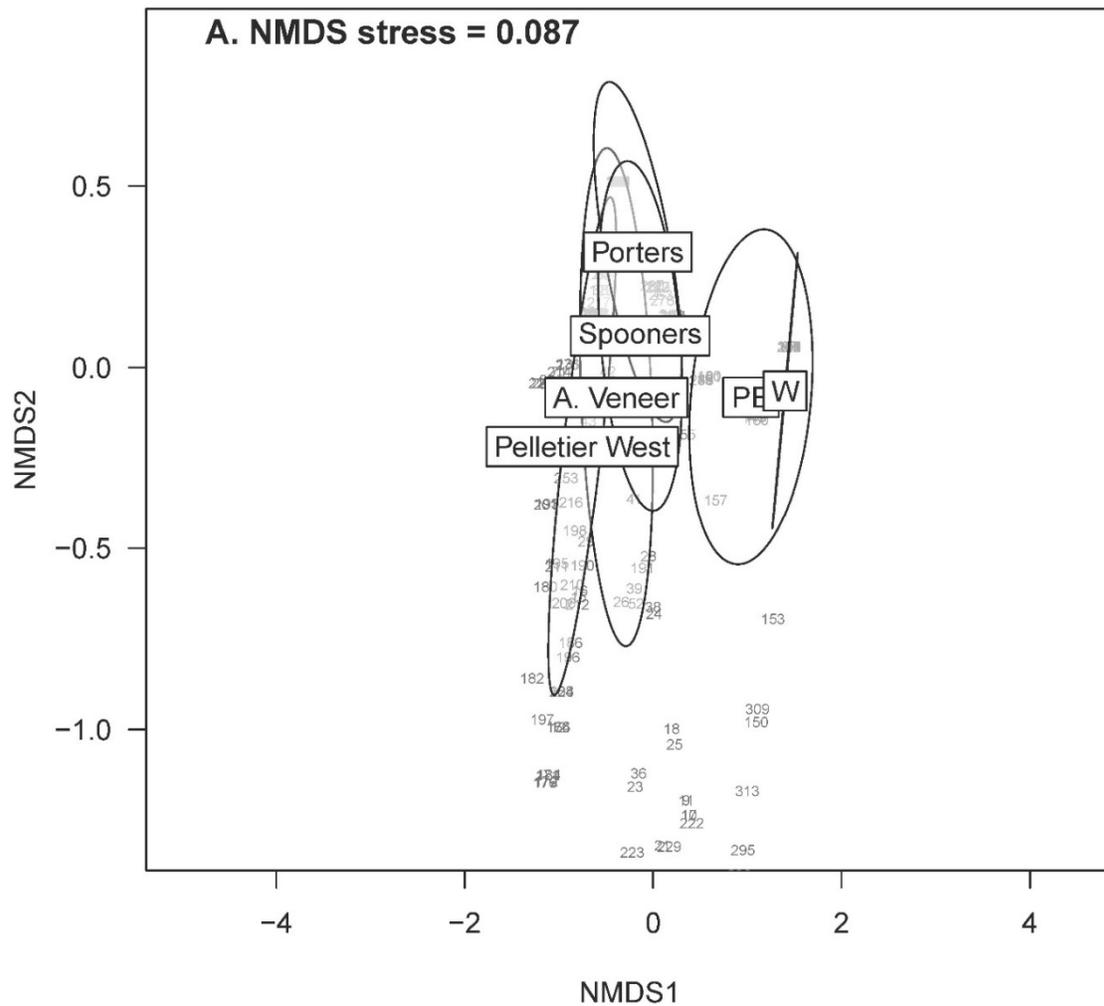


Figure 2.6. Non-metric multidimensional scaling ordination for 2013 minnow trap samples from six salt marsh creeks showing (A) sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses; (B) the direction and strength of fish and invertebrate catches that showed the greatest rank-correlation with sample dissimilarities; and (C) the direction and strength (length of the arrow) of continuous environmental/habitat variables, and the centroid (location) of each class of binary environmental/habitat variables most rank-correlated with sample dissimilarities. Samples from each trap deployment are the small gray numbers. The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). Creek labels correspond to ellipses from highest to lowest; ‘A. Veneer,’ ‘PE’ and ‘W’ in panel A are Atlantic Veneer, Pelletier East and Webb Creeks, respectively. ‘PctMarsh’ is percent of each creek’s high tide wetted area that is marsh.

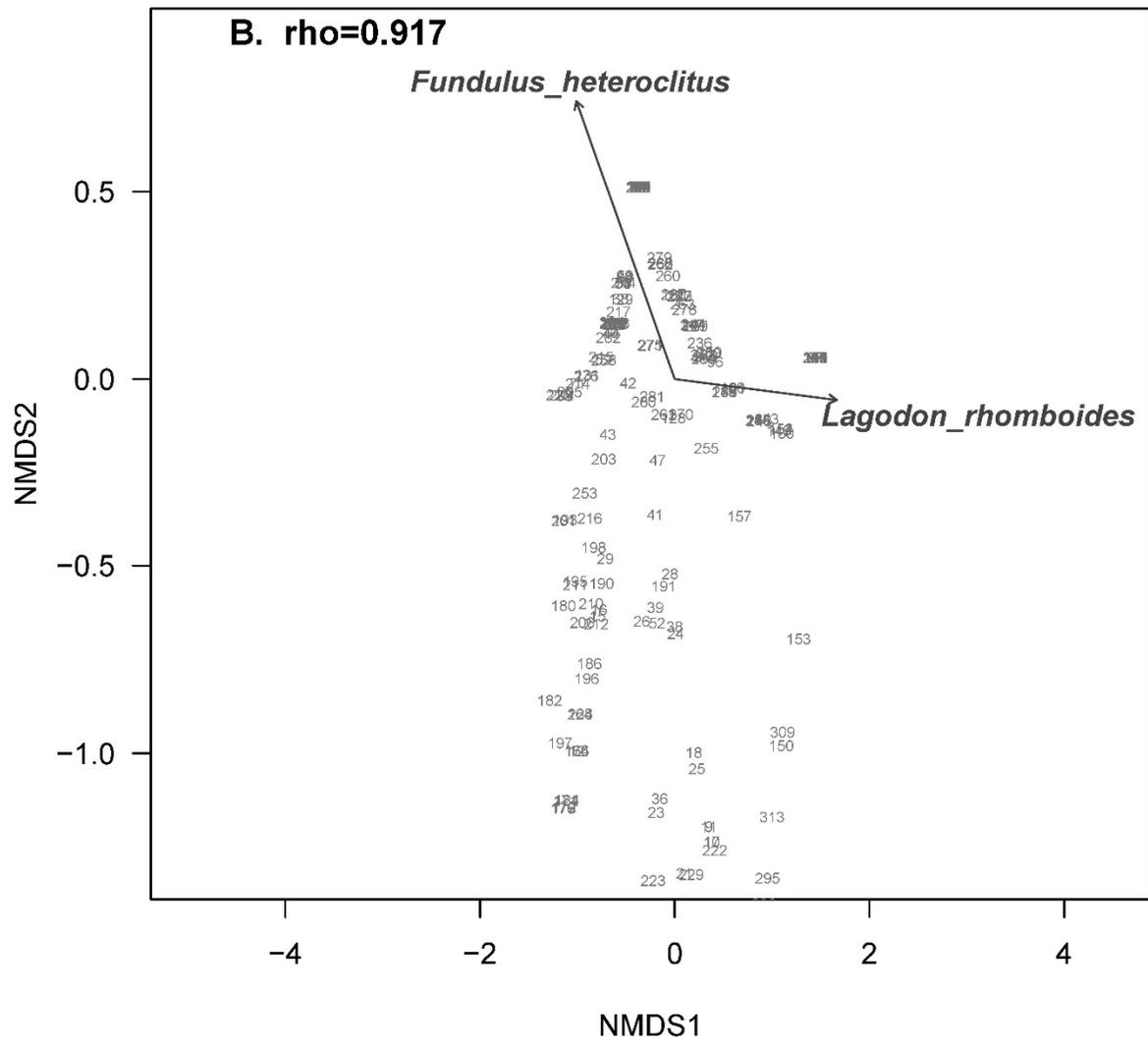


Figure 2.6 (con't)

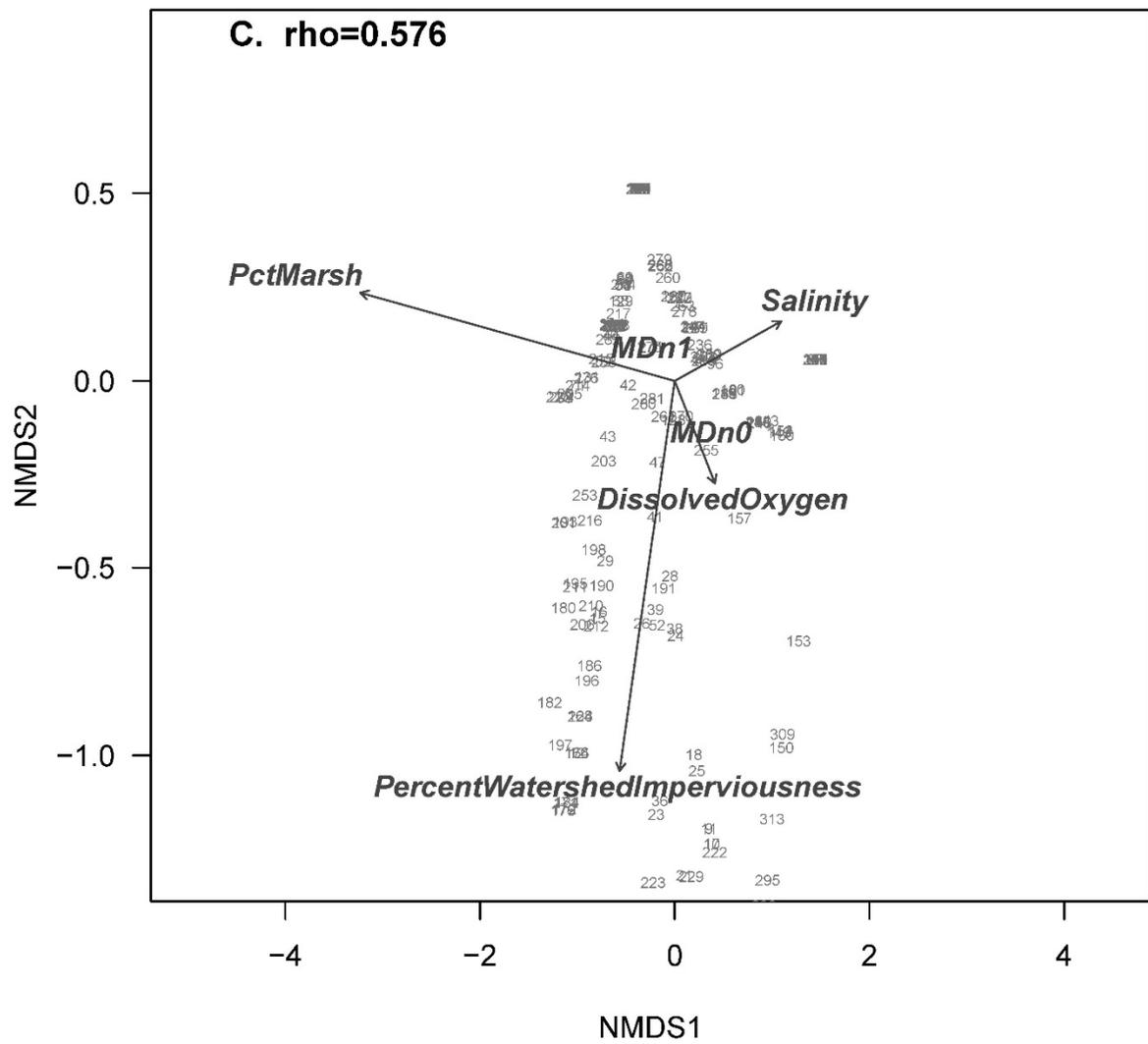


Figure 2.6 (con't)

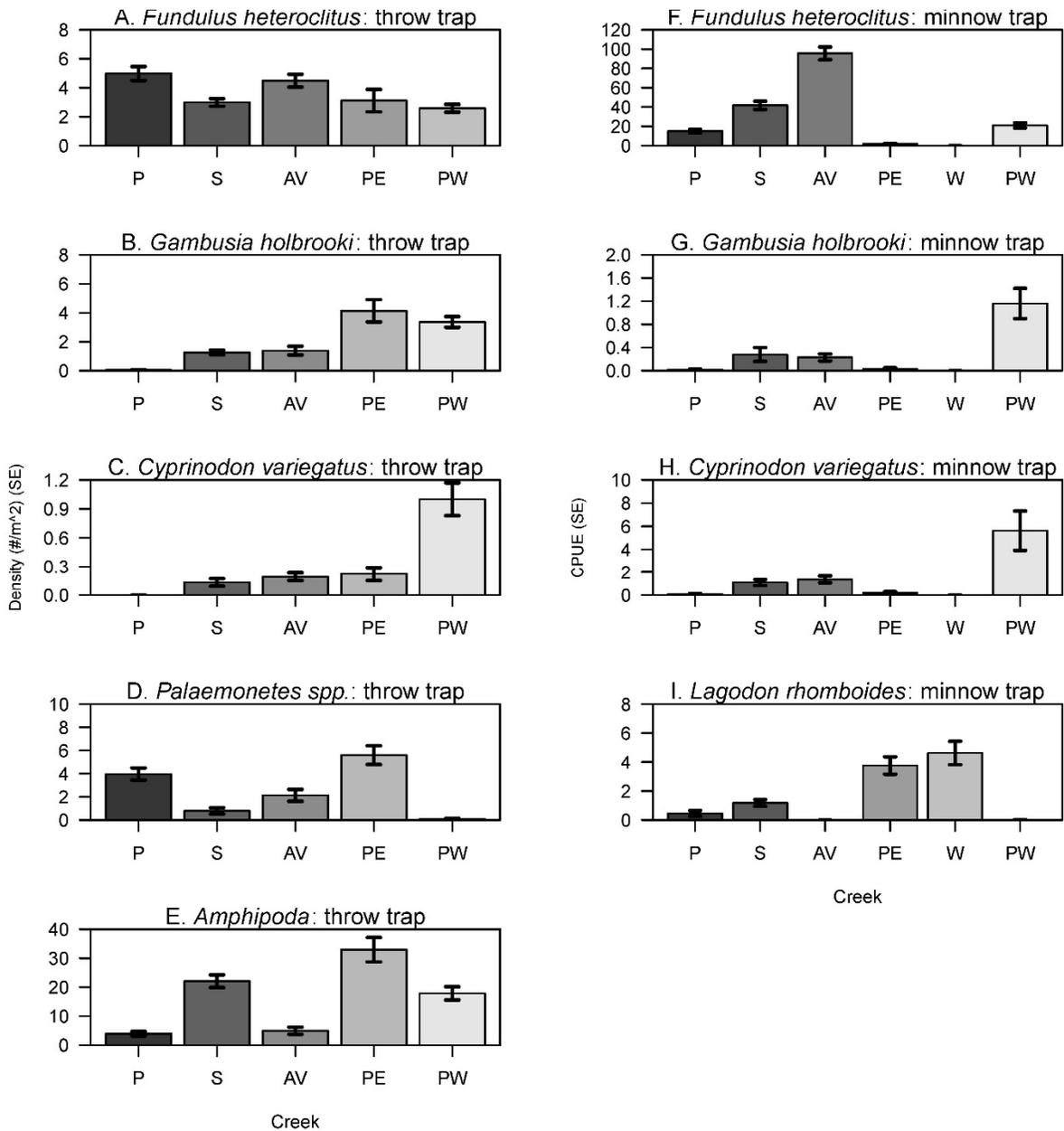


Figure 2.7. Mean density (individuals m⁻²) (\pm standard error (SE)) (y axis) of dominant nekton species collected with a 1 m² throw trap in five tidal creeks (x axis) (panels A-E), and catch-per-unit-effort (CPUE) (\pm SE) (y axis) of dominant macrofauna from wire mesh minnow traps set on 3-hour soak times in six tidal creeks (x axis) (panels F-I) sampled in coastal North Carolina in 2012 and 2013. Creeks are listed in order of increasingly greater watershed imperviousness on the x axis: Porters (P), Spooners (S), Atlantic Veneer (AV), Pelletier East (PE), Webb (W) and Pelletier West Creeks (PW). Throw trapping was not conducted in Webb Creek.

CHAPTER 3. FRAGMENTATION OF HABITAT AFFECTS COMMUNITIES AND MOVEMENT OF NEKTON IN SALT MARSH TIDAL CREEKS

Paul J. Rudershausen, Jeffery H. Merrell, and Jeffrey A. Buckel

ABSTRACT

The specific biological impacts of anthropogenic activities and associated fragmentation of estuarine habitats remain understudied. We compared nekton communities and fish movement at nine road crossings (with culverts) and a tenth crossing ('reference' crossing that lacked a road or a culvert) in first-order tidal creeks in coastal North Carolina. Sample sites were located within each tidal creek on both sides of each crossing. The dominant salt marsh fish *Fundulus heteroclitus* was batch-tagged to determine factors influencing its movement probability to sites on sides of crossings opposite from where it was tagged. Distance to the nearest marsh, shoreline armoring, and water depth were factors that most contributed to dissimilarities in biological communities among sample sites; *Fundulus heteroclitus* loaded on ordinations in a direction opposite of these urbanization effects while a dominant transient species *Lagodon rhomboides* loaded in a direction similar to these effects. The probability of *Fundulus heteroclitus* moving to sites on the opposite side of crossings from where it was tagged was positively related to the percentage of marsh-fringed shoreline within its published home range and was dome shaped in its response to water depth. The results emphasize the importance of preserving salt marsh immediately on each side of road crossings to maintain communities reflective of undisturbed habitats as well as movement rates of a dominant species in tidal creeks in the U.S. South Atlantic coastal plain.

INTRODUCTION

Habitat connectivity is an integral part of seascape structure and important for sustaining populations of estuarine nekton (Eggleston et al. 1999; Micheli and Peterson 1999; Roth et al. 2008). In the context of landscape or seascape ecology, connectivity is defined as ‘the degree to which the landscape facilitates or impedes movement among resource patches’ (Taylor et al. 1993). Connectivity has implications for habitat patch use by estuarine nekton (Micheli and Peterson 1999), the transfer of production from salt marshes (Kneib 2000; Stevens et al. 2006) and may explain a significant proportion of fish production in estuaries (Meynecke et al. 2008; Valentine-Rose et al. 2011).

Reduced connectivity between habitat patches, or fragmentation, represents an anthropogenic threat to biodiversity worldwide (Collinge 1996). Estuarine habitat fragmentation can be viewed as a change in the structural arrangement of patches (Peterson 2003) and can dramatically alter fish community composition in tidal creeks (Layman et al. 2004). Despite the importance of habitat connectivity, the influence of fragmentation in specific habitats and on specific taxa remains an understudied area of marine and estuarine ecology (Grober-Dunsmore et al. 2009). Understanding the effects of fragmentation in salt marshes is a particularly pressing issue since these ecosystems are among the most biologically productive on Earth (Barbier et al. 2011) and are lost at a rate of 1-2% annually worldwide (Duarte et al. 2008).

The health of estuaries needs to be viewed in the context of the landscape that surrounds them (Simenstad et al. 2002; Minello et al. 2003). Anthropogenic impacts to tidal creeks along the low-lying U.S. South Atlantic coast include not just changes to sub-tidal habitat features but also fragmentation of formerly connected habitats across intertidal areas

due to development such as road construction and shoreline armoring (Valentine-Rose et al. 2007a; Eberhardt et al. 2011; Lowe and Peterson 2014). Shoreline armoring of estuaries is an example of ‘structural fragmentation’ that eliminates intertidal salt marsh habitat (Peterson and Lowe 2009) and has been found to reduce the integrity (Bilkovic and Roggero 2008) and density (Torre and Targett 2016) of estuarine fishes near armored sites.

In addition to being structural, fragmentation can be hydrological, in which case the anthropogenic impediment to water flow also blocks the flow of organisms, matter, or energy (Valentine-Rose et al. 2007b). Road building and associated culvert placement is one example of hydrological fragmentation that poses a behavioral and physical deterrent to fish movement in both freshwater (Warren Jr. and Pardew 1998) and estuarine environments (Eberhardt et al. 2011).

Vegetated salt marsh is critical to the energy flow (Teal 1962) and ecology (Kneib 1997) of tidal creeks in the U.S. South Atlantic region. Water depth is an important determinant of nekton use of intertidal salt marsh creeks along the U.S. South Atlantic coast (Allen et al. 2007; Rudershausen et al. 2016) and metrics of channel morphology (such as water depth) influence nekton movement through these corridors (Rozas et al. 1988; Visintainer et al. 2006; Allen et al. 2007; Boström et al. 2011). Culverts, dredging and shoreline armoring are common impacts to salt marshes (Lee et al. 2006), deepen these inherently shallow creeks, and are assumed by North Carolina natural resource agencies to reduce the biotic integrity of North Carolina estuaries because they are a hydrological alteration (Jensen et al. 2014). However, state and federal natural resource agencies lack information on the extent of these human impacts in salt marshes (North Carolina Division of Marine Fisheries 2010; Environmental Protection Agency 2017). Despite the potential for

fragmentation to alter movement patterns of nekton, the specific effects of fragmentation on movement of estuarine nekton species remain largely unknown (Minello and Rozas 2002; Meynecke et al. 2008). The Atlantic coastal resident salt marsh fish *Fundulus heteroclitus* is responsible for exporting a significant proportion of biomass to higher-level predators in open-water estuaries (Kneib 1986; Cicchetti and Diaz 2002; Kneib 2000), fragmentation may compromise this export (Valentine-Rose et al. 2007; Valentine-Rose et al. 2011). Regional and national natural resource managers have identified the need for more fishery-independent information to help determine the effects of development on fish and invertebrate populations in North Carolina estuaries (North Carolina Division of Marine Fisheries 2010; Environmental Protection Agency 2017). This study contributes towards filling that need.

In this research we undertake metacommunity ecology, the study of multispecies interactions in patchy landscapes (Leibold et al. 2004). Here metacommunity ecology is used in an applied manner, an under-utilized approach that is useful for evaluating the consequences of management actions (Cadotte et al. 2017). We examine how fragmentation within tidal creeks influences nekton communities and whether culverts and instream habitat features influence the probability of *Fundulus heteroclitus* movement. For the community analyses, our goal was to determine if factors at small (within-creek) spatial scales contributed to differences in nekton community assemblages between paired sites in close proximity to each other. For the movement analyses, we sought to determine whether road culverts were barriers to connectivity or whether a dominant fish species could pass these culverts but elected not to due to site-specific habitat or anthropogenic factors. The fish's ability to move through a culvert thus defined whether a culvert or similar break in salt marsh habitat from development results in a loss of connectivity in these systems.

METHODS

Study sites We sampled from April 2015 through July 2016 in ten first-order tidal creeks in Carteret County, coastal North Carolina. The study creeks epitomize the patchiness of estuarine habitats located within a heterogeneous and developing coastal landscape (Boström et al. 2011). The sampled creeks are polyhaline, as salinities during non-rain events are generally greater than 20 psu (Rudershausen et al. 2016). The study areas are located in close geographic proximity and some are substantially altered due to development. Similar to Eberhardt et al. (2011), we defined a ‘crossing’ as a longitudinal segment of tidal creek where there was a culvert under a road or there was a reference segment of creek (no culvert). Thus, in this study each creek crossing consisted of a longitudinal creek segment whose length was the distance between fixed trap sample sites located immediately at each end of the segment. All but one of the ten crossings possessed a culvert (Figure 3.1; Table 3.1).

Crossings with culverts varied as to whether *Spartina alterniflora* salt marsh was present on both sides of the culvert or only on one side. The reference crossing had salt marsh on both sides. Among the ten creeks and twenty sites that were sampled, as well as other areas along the U.S. South Atlantic coast, reduced or eliminated salt marsh at a site can be a consequence of shoreline armoring (bulkheads) (Kennish 2001; Gittman et al. 2015), dredging (Kennish 2001), and culvert scour that often widens and deepens sub-tidal habitats adjacent to culverts (Wargo and Weisman 2006; pers. obs.). The distance from each sample site to the nearest patch of salt marsh was zero on both sides of six crossings. For the other four crossings sampled for communities, this distance was zero on one side of the crossing

but greater than zero on the side of the crossing lacking physical connectivity to salt marsh (Table 3.1).

The nine culverts across which we sampled typify those found bisecting tidal creeks in coastal North Carolina. The culverts were not perched (i.e., the bottom of the full length of each culvert remains covered with water at low tides). Most of the culvert crossings exhibited scour pools at the downstream sample site except for Wading Creek (scour pools at both the upstream and downstream sample sites) and Town Creek (no obvious scour pools from the culvert).

We measured multiple anthropogenic and habitat features that had the potential to influence community structure and the probability of *Fundulus heteroclitus* movement. Fixed factors recorded at each site included percent fringing salt marsh (described below), presence/absence of salt marsh connected to a site, presence/absence of shoreline armoring at a site, and water depth. Culvert length, a shared metric between the two sites in each of nine creeks, was also recorded. Current velocity at each crossing, over both ebb and flood tides, was measured with a General Oceanics model #2135 flowmeter (General Oceanics, Inc., Miami, FL). Culvert length and water depth are two factors that have been identified as affecting the composition of nekton communities and movement at broader (creek-wide) spatial scales in Atlantic coastal tidal creeks (Eberhardt et al. 2011; Allen et al. 2007).

We used the percent of vegetated marsh edge above upstream sample sites and below downstream sample sites as a metric of marsh integrity (Baltz et al. 1993). We measured the combined percentage of marsh that fringed both shorelines to a distance of 200 m away from each site. This 200 m distance (via meander of each creek) was selected because it represents an approximate maximum home range distance (Skinner et al. 2005) for the

dominant salt marsh fish species in this region, *Fundulus heteroclitus* (Able and Fahay 1998). The length of each crossing (distance between sample sites) was far less than the published home range distance of *Fundulus heteroclitus*, increasing the probability that any patterns we observed for *Fundulus heteroclitus* would not be due to the limited dispersion of this species. Each crossing had 100% marsh edge at the upstream sample site except Wading Creek. The percentage of edge at the downstream sample site varied among crossings. The exception was Wading Creek, where the downstream sample site had 100% marsh edge but the upstream site largely lacked edge within the home range of *Fundulus heteroclitus*.

Nekton sampling for effects of habitat fragmentation on community structure Each site was sampled with Gee-style wire minnow traps possessing 6.4 mm square mesh and baited with whole dead *Brevoortia tyrannus*. Traps were fished roughly twice per month over 24 h periods from April 2015 through July 2016. Exceptions to trap sampling occurred in instances of lost or opened traps, which were not counted, and three crossings that were first sampled after the study started; Bridges Creek was first sampled in August 2015 while Goose and Wading Creek crossings were first sampled in March 2016. During each 24 h soak time we deployed one trap in the sub-tidal creek channel at the upstream and downstream ends of each culvert. In the case of the reference crossing, traps were deployed a distance apart from each other that was an approximate average distance separating sites at the culvert crossings (Table 3.1). At the conclusion of each trap deployment, trapped individuals were identified, counted, and released (except for tagged *Fundulus heteroclitus*, see below). Most individuals were identified to species. Some individuals were identified to genus or family levels in instances where multiple closely related species in a higher order taxa were known to occur

in this geographic region (e.g., *Gobiosoma* spp., *Mugil* spp., *Eleotridae*, *Palaemonetes* spp., *Farfantepenaeus* spp. and Xanthidae).

Like all sampling gears, minnow traps are size-selective. By virtue of the sizes of their trap meshes and funnel entrances, respectively, minnow traps have lower and upper limits of size selectivity. However, the Gee-style minnow trap is nonetheless a gear type by which numerous salt marsh nekton species can be sampled to measure relative abundances while minimally disturbing habitat (Talley 2000; Rudershausen et al. 2016). Minnow traps retain fishes roughly 40 - 110 mm total length, depending on species (West and Zedler 2000; Teo and Able 2003; Rudershausen et al. 2016), and invertebrates over roughly the same size range (pers. obs).

Sampling for Fundulus heteroclitus movement past crossings We estimated movement probabilities of adult *Fundulus heteroclitus* past the ten study crossings. The process to estimate movement probability involved batch-tagging *Fundulus heteroclitus* caught after each 24-hour soak time of minnow traps set above and below each crossing. Over each sampling visit to a crossing fish from the upstream site were tagged with a different color of Visible Implanted Elastomer (VIE) tag (Northwest Marine Technology, Shaw Island, WA) than fish from the downstream site. In addition to using different tag colors we tagged fish in different body locations to among the sample visits to each crossing so some colors could be re-used. The range of total lengths of individuals that were VIE tagged widely overlapped between the two sides of each crossing and also among crossings. Tagged fish were released back to the site from which they were captured. Over subsequent sampling after 24 hour trap soak times events we examined *Fundulus heteroclitus* for tags of specific colors and tagging body locations and recorded the total number of tagged individuals of each tag color/body

location at each sample site. Using this information, we classified each recaptured fish as a mover (to the opposite side of the crossing from where it was tagged) or a non-mover.

Analyses of nekton communities We tested for differences in nekton communities among site types and determined habitat and anthropogenic factors most responsible for differences.

The community analysis was done for data collected over the full study period (when not all creeks were sampled in early months). It was also done for the portion of the study (March – July 2016) when data were collected simultaneously in all ten creeks in order to determine whether the results changed compared to analyzing the full data set collected over the entire study period. In addition to the community analysis, catch rates of each dominant species were compared among the three site types using one way analysis of variance (ANOVA) on logarithmically-transformed data ($\ln(x+1)$) and using the Tukey HSD post-hoc test for pairwise comparisons between site types.

The community analysis was conducted in several steps. First, we used published studies (Bretsch and Allen 2006; Allen et al. 2007; Bilkovic 2011; Rudershausen et al. 2016) that have identified important habitat and physical determinants of tidal creek nekton communities along the southeastern U.S. coast (salt marsh, shoreline armoring and water depth) to separate sites into three groups. These three groups were 1) sites that lacked a culvert and had no visible physical impact ('reference'), 2) sites with a culvert next to them but otherwise having no impact ('non-impacted'), and 3) sites with a culvert and obviously impacted by development (reduction or complete loss of salt marsh from one or more causes and/or obvious change in creek morphology) ('impacted') (Table 3.1). We focused our sampling effort on crossings with one or more types of development to better understand their effects on nekton communities and movement. Previous research on nekton community

structure and movement in salt marsh habitats and reference crossings (Rudershausen et al. 2014; Rudershausen et al. 2016) suggests that results from the single reference crossing researched in this study would likely to be similar for other reference crossings in this region.

Non-metric multi-dimensional scaling (NMDS) was used to graphically depict the community of nekton captured for each of the three site types. NMDS is an ordination technique well suited for visualizing non-normal or discontinuous data in two-dimensional graphical space (Clarke 1993; McCune and Grace 2002). The NMDS algorithm seeks to minimize stress, a measure of fit that determines how well the Euclidean distances preserve sample dissimilarities (Kruskal 1964; McCune and Grace 2002).

We conducted NMDS with each individual trap sample as its own community (data point) in the ordination. The Bray-Curtis coefficient was used to construct similarity matrices for the sample-by-species matrix on counts of individuals from minnow trap collections, which were square-root transformed to diminish the influence of numerically dominant taxa. Poos and Jackson (2012) discuss criteria for including vs. excluding rare species in multivariate assessments; these authors state that the removal of rare species from the ordination analysis may affect the interpretation of results in ecological studies as well as discard information on less commonly encountered species that may be more susceptible to and indicators of ecosystem stress. We elected to balance the inclusion vs. exclusion of rare species by conducting NMDS on species that occurred in at least 1% of the collections across all three site types. While each individual trap was considered a 'sample' for NMDS, traps with a zero catch across all taxa that met the 1% inclusion threshold cannot be evaluated and thus were eliminated from the analysis. Stress was computed as part of the NMDS. Stress levels $< \sim 0.2$ are considered reasonable while levels $> \sim 0.2$ can potentially lead to

misinterpreting scaling distances (Clarke and Warwick 2001). Following ordination model runs we constructed NMDS plots depicting the centroid and standard deviation ellipse of each site's community.

Following NMDS, Analysis of Similarity (ANOSIM) was conducted to provide a quantitative interpretation of whether biological communities differed between the two sites at each creek. Increasingly more positive values of the ANOSIM test statistic, R , indicate greater differences in fish community among sites while an R value of 0 indicates no dissimilarities among sites (Chapman and Underwood 1999). Significant p -value (≤ 0.05) for R but a low value ($< \sim 0.2$) indicates effects that are relatively unimportant (compared to higher R values) and can be a result of large sample sizes. Similarity percentage (SIMPER) analysis was conducted to determine the most influential taxa contributing to the overall Bray-Curtis dissimilarity between pairs of communities (McCune and Grace 2002).

In conjunction with NMDS, we determined whether the number of samples collected at each site was sufficient to describe the community there. This was done by computing a pseudo multivariate dissimilarity-based standard error (*multSE*) (Lefchek 2015) and determining at what level of sampling at each site the error about the *multSE* value overlaps with the computed error for the final (highest) number of samples integrated into the multivariate analysis (in this case, NMDS) (Anderson and Santana-Garcon 2015). This analysis was implemented through the *multSE* function (Lefchek 2015) run through R software (R Development Core Team 2015).

We tested for the influence of habitat and anthropogenic factors on nekton communities using the nonparametric BIOENV approach (Clarke and Ainsworth 1993). The method determines the suite of environmental and habitat factors that have the greatest rank

correlation with sample dissimilarities of the biological community that the researcher analyzes through ordination. We conducted the BIOENV analyses using a “forward selection/backward elimination approach” where the rank correlation of sample dissimilarities between a subset of environmental variables/taxa and the full data set of environmental variables/taxa was set at 0.95 (Clarke and Warwick 1998). Euclidean distances among sample items were calculated as part of each BIOENV procedure; this distance measure can be applied to both categorical and continuous environmental/habitat data (McCune and Grace 2002). A non-parametric Spearman rank correlation coefficient (*rho*) is calculated for each suite of habitat and anthropogenic factors. After the group of best-fitting factors is determined (greatest *rho* value), they can be plotted in NMDS ordination space. Each continuous environmental/habitat factor in the most parsimonious BIOENV model is plotted as a vector while each level of a categorical factor is plotted as a point.

The non-parametric, distribution-free nature of the BIOENV test allows the researcher to test various combinations of closely related factors to visualize how they load on the ordination. We considered a variety of factors in the BIOENV analysis. These were percentage of vegetated marsh edge within the *Fundulus heteroclitus* home range, the distance from the trapping site to the nearest patch of salt marsh on the same side of the crossing, water depth, and the presence/absence of salt marsh, and presence/absence of shoreline armoring (bulkhead). These variables were all considered due to the potential for taxa to respond differently to fragmentation and at different spatial scales (Eggleston et al. 1998; Minello and Rozas 2002). Following the determination of the best-fitting suite of environmental/habitat factors, a permutation test was used to determine whether each factor

in the most parsimonious BIOENV model was significantly rank-correlated ($\alpha = 0.05$) with ordination sample dissimilarities.

BIOENV can also be conducted with biological data. In this study we used this approach to determine the group of taxa that showed the greatest rank correlation with sample dissimilarities. Each taxon in the best fitting BIOENV analysis was plotted as a vector. The NMDS ordination, BIOENV, fitting of environmental/habitat variables and taxa, and permutation tests were conducted with *R* software (R Development Core Team 2015) using the *vegan* package (Oksanen et al. 2016).

Analysis of Fundulus heteroclitus movement We sought to identify factors influencing *Fundulus heteroclitus* movement past the ten crossings sampled in this study. This process involved fitting binomially distributed random-intercept generalized linear models (generalized linear mixed models: GLMMs) with logit links. Mixed models allow the researcher to extend the model results from studies with at least 5-10 study ‘subjects’ to a larger population of ‘subjects’ (in this case, tidal creek crossings) that have similar characteristics (Kéry 2010).

For the data to which GLMMs were fitted, C (number of successes) represented the number of tagged individuals that had subsequently moved to the side of a crossing opposite from the side on which they were tagged and released while N (number of trials) represented the total number of recaptured individuals of a single tag color and body location (fish that were tagged at a single site on a single visit to a crossing), regardless of whether they moved or not. There were multiple sampling events to tag fish at each site and unique combinations of tag color and body location were used for each sampling event. C was assumed to conform to an underlying binomial distribution (see Kéry 2010) with success probability p .

For each crossing we only used C and N data for the first sampling visit that a unique tag color/body location combination (from a single tagging event) was recaptured. This insured that data from the same individual was not used twice in the analysis and reduced the chances that some recaptured individuals had made round-trip movements without intervening recapture on the side of a crossing opposite the side at which they were originally tagged.

We incorporated directionality of movement into the model fitting. For fish tagged at the downstream site at a crossing, C was defined as the number of individuals of a unique tag color/body location that had moved upstream. Similarly, for fish tagged at the upstream site, C was defined as the number of individuals of a unique tag color/body location that had moved downstream.

Before model fitting to *Fundulus heteroclitus* movement data we initially considered numerous characteristics of the sites and crossings. Data for site-specific covariates considered in GLMMs fitted to *Fundulus heteroclitus* movement data were for the side of the crossing that C individuals moved to (the side opposite from which they were tagged and released). Site-level covariates initially considered included the presence/absence of salt marsh at each site, the percentage of vegetated marsh edge within the *Fundulus heteroclitus* home range of each sample site, and water depth.

Other covariates initially considered in models fit to *Fundulus heteroclitus* movement data were attributes of the crossing separating the two sites and thus had a shared value between the two sites at each crossing: crossing length and current velocity. Culvert length and water current velocity through culverts have been identified as negatively affecting rates of fish passage in freshwater creeks (Love and Taylor 2003) and high current velocity has been found to negatively affect movement of *Fundulus heteroclitus* in New England tidal

creeks (Eberhardt et al. 2011). For current velocity we averaged the values across ebb and flood tidal currents at each crossing.

Collinearity between pairs of factors potentially explaining fish movement was examined with Spearman rank correlation (when one factor in a pair was categorical) or the Pearson correlation coefficient (when both factors in a pair were continuous). The presence/absence of salt marsh at each site and percent of marsh edge within the published *Fundulus heteroclitus* home range were strongly correlated (Spearman $r = 0.537$, $p < 0.001$); marsh presence/absence was dropped from further consideration in favor of percent marsh edge in the *Fundulus heteroclitus* home range due to potential movement of this species not just to specific sample sites but over wider home range areas (Skinner et al. 2005). Percent marsh edge within the *Fundulus heteroclitus* home range and culvert length were inversely correlated (Pearson $r = -0.254$, $p = 0.017$) owing to the fact that less developed marsh mosaics in this region are more likely to be bisected by narrower roads (pers. obs.). However, this relationship was weak (low absolute value for the correlation coefficient) so we retained both factors. Percent marsh edge within the *Fundulus heteroclitus* home range and site water depth were found to be inversely correlated (Pearson $r = -0.751$, $p < 0.001$) owing to a typical pattern along the U.S. Atlantic coastal plain whereby water depth increases with anthropogenic conversion of salt marshes to developed shorelines (Hartig et al. 2002). For this reason these two factors were not included in the same model but were included in separate model runs owing to the importance of each of them in dictating movements and abundance of tidal creek species (Allen et al. 2007; Rudershausen et al. 2016). Current velocity and crossing length were not included in the same model because they were negatively correlated (Pearson $r = -0.731$, $p < 0.001$). However, current velocity and

crossing length were incorporated into each of the two full models. Each of these four factors was also tested alone in its own model.

Observed rates of movement displayed a linear pattern with percent marsh edge within the *Fundulus heteroclitus* home range but a dome-shaped relationship with water depth, current velocity and crossing length. Thus, models fitted to movement data simultaneously incorporated linear and quadratic terms for water depth, current velocity and crossing length, respectively, and just a linear term for the percentage of vegetated marsh edge within the *Fundulus heteroclitus* home range. Before model fitting (outside of each model run) we centered the values for each covariate and centered the squared values for the water depth, current velocity and crossing length covariates, a technique that improves the efficiency of the Markov Chain Monte Carlo sampler when running a probabilistic model (McCarthy 2007).

The eight GLMMs of *Fundulus heteroclitus* movement as well as a null (intercept-only) model were fitted via Bayesian inference using published prior probability distributions and likelihoods (Kéry 2010). For the linear predictor portion of the model, a normal prior probability distribution was assigned to the random intercepts (*alpha*) term that, in turn, was specified by hyper-parameters for the grand mean rate of movement among the ten creeks, *mu.int*, and precision, *tau.int*, the inverse of variation among creeks. In turn, *mu.int* had an uninformative normal prior probability distribution (mean = 0, precision = 1×10^{-6}) and *tau.int* was calculated as the inverse of the squared value of the standard deviation of the random intercepts term, *sigma.int*, which had an uninformative uniform prior probability distribution (minimum = 0, maximum = 100). Finally, an uninformative normal prior

probability distribution (mean = 0, precision = 1×10^{-6}) was given to each partial regression coefficient (*beta*) for each covariate in each model (Appendix A).

Each GLMM was fitted by calling *JAGS* software version 4.0 (Plummer 2015) from *R* software using the package *R2jags* (Su and Yajima 2015) and run using three chains of initial values updated 100,000 times. Every 10th observation was retained and the initial 10 percent of retained updates were discarded as burn-in. Convergence was determined by computing the Gelman-Rubin statistic for each model parameter; values $< \sim 1.1$ for this statistic suggest adequate convergence to a stable posterior probability distribution (Gelman 1996).

The goodness of fit for each model fitted to *Fundulus heteroclitus* movement data was assessed by determining a Bayesian probability (p) value (Gelman et al. 1996) (Appendix A). Computing a Bayesian p-value involves constructing a replicate data set using parameter estimates obtained from the model fitted to the actual data (Kéry 2010). Chi-square was used as the discrepancy (goodness of fit) measure for both the actual and replicated data sets. This p-value computes the proportion of instances when the chi-square value for replicated data set exceeds that for the actual data set; Bayesian p-values of ~ 0.5 suggest an adequate model fit while values near 0 or 1 suggest a poor fit of the model to the data (Kéry 2010).

We used the Bayes factor (*K*) as a method of comparing the parsimony of mixed models (Kass and Raftery 1995; Rouder et al. 2012) between each of the eight models that contained covariates and the null model. We did not use the Deviance Information Criterion (DIC) as a tool for model selection because it is believed to be a poor choice when fitting mixed models (Hooten and Hobbs 2015). The value for *K* for each model containing

potential explanatory factors (relative to the null model) was computed using the function *lmBF* in the R package *BayesFactor* (Morey et al. 2015). Values for *K* in the range of 0-1, 1-3, 3-20 and >20 respectively indicate negative, inconsequential, positive, and strong support for a model (Kass and Raftery 1995).

RESULTS

Analysis of nekton communities A total of 500 trap samples were collected from the 20 sample sites. Of these, 32 traps were empty, resulting in 468 samples that were analyzed for community composition with NMDS. The number of replicate samples at each site adequately characterized the community; multivariate dissimilarity-based standard error calculations revealed that the estimated minimum number of samples needed to characterize the community was exceeded for each site.

Two taxa dominated collections from the ten crossings studied for community structure. Taken together, the fish species *Fundulus heteroclitus* and *Lagodon rhomboides* comprised 93.3% of all individuals. Mean catch rates differed among sites for both *Fundulus heteroclitus* ($F = 113.3$, $p < 0.001$, residual degrees of freedom (df) = 465) and *Lagodon rhomboides* ($F = 41.2$, $p < 0.001$, df = 465). The contribution of each of these two species to the community differed markedly between reference and impacted sites as well as between non-impacted and impacted sites ($p < 0.001$ in each case), but not between reference and non-impacted sites (*Fundulus heteroclitus*, $p = 0.968$; *Lagodon rhomboides*, $p = 0.470$) (Figure 3.2).

Thirteen taxa exceeded the threshold frequency of occurrence for inclusion in ordination modeling. These taxa were the fishes *Fundulus heteroclitus*, *Lagodon rhomboides*, *Cyprinodon variegatus*, *Gambusia holbrooki*, *Gobiosoma* spp., *Anguilla*

rostrata, *Mugil* spp., *Leiostomus xanthurus* and *Eleotridae*, as well as the crustaceans *Palaemonetes* spp., *Callinectes sapidus*, *Farfantepenaeus* spp. and Xanthidae spp.

ANOSIM results comparing communities between pairs of site types showed that the community composition overlapped between reference and non-impacted sites (ANOSIM $R < 0.2$) even though the p-value for this ANOSIM test statistic was marginally significant ($p = 0.046$; Table 3.2). Relatively high ANOSIM R values (> 0.2) as well as significant p-values for these test statistics indicated less overlap between reference and impacted sites, and between non-impacted and impacted sites, respectively. NMDS plots also showed more overlap between reference and non-impacted sites than between each of these site types and impacted sites (Figure 3.3A). The ordination stress was reasonably low (0.158). SIMPER analysis revealed that *Fundulus heteroclitus* was the most influential species contributing to sample dissimilarities for each pair of site types (Table 3.2).

The NMDS, ANOSIM and SIMPER results were largely similar when model fitting to the data collected simultaneously in all ten creeks (March - July 2016). The one exception was that the ANOSIM R value was not significant ($p = 0.070$) when communities were compared between reference and non-impacted sites using the reduced data set.

The BIOENV analysis of environmental and habitat variables revealed that three factors were included in the model that showed the greatest rank correlation (Spearman $\rho = 0.172$) with sample dissimilarities of the nekton community. Distance to the nearest marsh and water depth at each site were continuous factors in this best-fitting model while the presence/absence of bulkheads was a binary factor in this model (Figure 3.3B). Permutation testing found that each of the three factors in this model was significantly rank-correlated ($p < 0.01$) with ordination sample dissimilarities. The results were similar when BIOENV

models were fitted to the reduced data set collected simultaneously in all 10 creeks (March – July 2016); the presence/absence of bulkheads was the only one of the three aforementioned habitat/urbanization factors not in the model that best fitted the reduced data set.

The BIOENV analysis of species included in the NMDS ordination found that nine taxa were in the model that showed the greatest rank-correlation with sample dissimilarities (Spearman $\rho = 0.762$) (Figure 3.3C). The two dominant species, *Fundulus heteroclitus* and *Lagodon rhomboides*, were part of this suite of taxa and loaded on the ordination at roughly equal strengths but in different directions. *Fundulus heteroclitus* loaded a direction similar to samples from reference and non-impacted sites that were typically shallow and close to marsh habitat. In contrast, *Lagodon rhomboides* loaded in a direction similar to impacted samples, which were typically deeper, possessed armored shoreline (e.g. bulkheads) and were further removed from salt marsh. None of the other eight taxa in the best-fitting model loaded in a direction similar to *Fundulus heteroclitus* or *Lagodon rhomboides*. *Palaemonetes* spp., a dominant crustacean taxa in tidal creeks in this region (Welsh 1975), loaded in a direction similar to samples from deeper sites but at an intermediate distance to the salt marsh. The majority of the six other taxa in the best-fitting model loaded in a direction generally similar to *Palaemonetes* spp. (Figure 3.3C) but were more closely associated with shallower sites closer to the nearest salt marsh than *Palaemonetes* spp. The BIOENV results on important taxa loadings were similar when models were fitted to data collected over the period when all ten creeks were sampled simultaneously (March - July 2016); the same nine taxa were included in the ordination model when fitting to the full and the reduced data sets and *Gambusia holbrooki* was an additional species in the model that best fitted the reduced data set.

In summary of the multivariate analyses, the results showed that impacted sites had nekton communities dominated by *Lagodon rhomboides*. These were anthropogenically deepened sites further removed from salt marsh due to pronounced scour and/or having altered shoreline (e.g., bulkheads) (Figure 3.2; Figure 3.3B). In contrast, communities at the reference and non-impacted sites were dominated by *Fundulus heteroclitus*; these sites were further removed from metrics of anthropogenic disturbance on ordination plots.

Movement of Fundulus heteroclitus A total of 2,311 *Fundulus heteroclitus* were batch tagged to study movement of this species past tidal creek crossings. There were 96 sampling events that had recaptured *Fundulus heteroclitus* whose markings were tag colors/body locations from a unique batch tagging event that had not previously been recaptured at each crossing (n = 285 recaptures). There was generally high variability in rates of *Fundulus heteroclitus* movement past each crossing (Figure 3.4).

Seven of the eight movement models that included covariates each had values for Bayes factors (K) that showed either positive or strong support relative to the null model (Table 3.3). The two covariates that consistently (i.e. in multiple models) had coefficients with 2.5 and 97.5 credible intervals that did not overlap with zero were percent marsh within the home range of *Fundulus heteroclitus* (Table 3.3; Figure 3.5A) and water depth (Table 3.3; Figure 3.5B). Percent marsh had a positive effect on movement probability while movement rates to the shallowest and deepest sites were lowest with higher rates of movement at intermediate depths. Thus, mummichogs were willing to move through the culvert types in our study as long as the habitat on the opposite side of a crossing contained marsh and was not too shallow or too deep. Bayesian p-values for each model suggested

reasonable fit although some values were ~ 0.3 . The convergence statistic for each estimated parameter indicated adequate convergence to a stable posterior distribution.

DISCUSSION

This study sought to fill a data gap identified by state and federal natural resource planners charged with protecting critical salt marsh ecosystems by testing the influence of common causes of salt marsh fragmentation (elimination of marsh, dredging, shoreline armoring, and culvert placement) on tidal creek nekton communities and movement rates of a dominant species. Determining the influence of habitat connectivity on nekton communities and movement is valuable information for resource managers intent on preserving the biological productivity of salt marshes (Kneib 1997).

The natural habitat and alteration characteristics of crossings sampled in this study are largely representative of those found along the low-relief U.S. South Atlantic coast. Thus, the results from this study are applicable to other micro-tidal areas of this coastline. Other than the Eberhardt et al. (2011) and Bowron et al. (2011) studies, most research on fish passage through culverts has been in freshwater systems possessing unidirectional flow (Warren Jr. and Pardew 1998; Poplar-Jeffers et al. 2009) that, as non-tidal systems, have impediments to movement (e.g., stream gradient, culvert slope, and culvert perch) that generally do not apply to tidal creek crossings or culverts in the U.S. South Atlantic coastal plain.

Fragmentation of salt marsh influences nekton community assemblage The presence/absence of *Spartina alterniflora* salt marsh determined nekton communities over spatial scales smaller than the home range of *Fundulus heteroclitus*. Crossings with sites lacking connectivity to marsh as well as sites further removed from the nearest marsh possessed

different community assemblages and lower percentages of marsh residents on the impacted sides of these crossings. Thus, the impacts of urbanization appear to be species-specific in tidal creeks (Layman et al. 2004; Krebs et al. 2014). These results are also consistent with a recent creek-wide analysis of community data in many of these same study creeks that found that salt marsh attributes (e.g., percent marsh) were important factors underpinning community differences at creek-wide spatial levels (Rudershausen et al. 2016; Chapter 2). At sites that lacked connectivity in this study, a dominant species and obligate marsh resident, *Fundulus heteroclitus*, was replaced by *Lagodon rhomboides*. *Lagodon rhomboides* was the dominant transient species in this study and a habitat generalist (Jordan et al. 1996). Ordination results for *Callinectes sapidus* and *Palaemonetes* spp., crustaceans important to salt marsh trophic dynamics (Welsh 1975; Kneib and Knowlton 1995; Silliman and Bertness 2002), suggest that they also respond to common types of instream development pressures in salt marsh systems. This is consistent with recent studies that have found that shoreline armoring reduces the habitat value for *Callinectes sapidus* (Long et al. 2011) and that intact salt marsh mosaics support greater abundances of *Palaemonetes* spp. than impacted marsh systems (Lowe and Peterson 2014).

Factors influencing the abundance of *Fundulus heteroclitus* at sample sites were consistent with factors influencing its movement probability. This species had low or zero rates of movement to sites with reduced percentages of salt marsh or elimination of this habitat. In contrast to our findings, Eberhardt et al. (2011) found that culvert presence and hydrological regime did not affect tidal creek fish communities collected from the upstream side of New England road crossings relative to reference crossings; however, they did not sample artificially deepened scour pools given their gear type used (fyke nets). Eberhardt et

al. (2011) did not mention whether the salt marsh mosaics sampled in that study were intact or altered at each of their sample sites.

Any management efforts to maintain the landward-to-seaward connectivity among marsh patches are likely to help maintain communities of marsh residents in these and similarly configured estuaries and thus sustain the ‘trophic relay’ (Kneib 1986; Kneib 2000; Stevens et al. 2006) by marsh-resident nekton to higher-level predators in nearby open-water estuaries. A recent community analysis of nekton in Gulf of Mexico estuaries similarly concluded that preserving the functional connectivity among marsh patches helps maintain communities and secondary production reflective of undisturbed salt marsh mosaics (Lowe and Peterson 2014).

The multivariate community analysis included common habitat and development features to test their influence on how communities separated in ordination space. Some of these features are widespread anthropogenic disturbances in North Carolina tidal creeks (Jensen et al. 2014) and other tidal creeks along the U.S. coastline (Kennish 2001; Holland et al. 2004; Lowe and Peterson 2014), and were part of the BIOENV model that best correlated with community dissimilarities. One of these disturbances was distance to the nearest marsh habitat from each sample site. Among sites sampled in this study, this distance is greater than zero due exclusively to anthropogenic activities that have eliminated salt marsh. Anthropogenically-eliminated salt marsh and shoreline armoring are ‘cost’ factors that are assumed to negatively affect estuarine nekton populations in North Carolina (Jensen et al. 2014) and our results support this assumption.

There are several common construction types that can lead to reduced area of salt marsh in tidal creeks along the U.S. South Atlantic coast. Bulkheads are commonly used

structures to armor shoreline (Gittman et al. 2015). These structures fragment salt marsh and reduce the diversity and integrity of estuarine fish communities (Peterson et al. 2000; Bilkovic and Roggero 2008; Peterson and Lowe 2009). Water depth at each site was also a factor in the best-fitting BIOENV model; increased depth at the sites we sampled most often results from dredging to create boat basins and from scouring due to water flow through inappropriately-sized or shaped culverts (Wargo and Weisman 2006).

Community differences at our sampling sites could result from habitat-specific attributes but could also be influenced by the ability of fish to move to those sites. That is, culverts may impede movements to upstream or downstream locations. As described in the next section, the movements of *Fundulus heteroclitus* through culverts suggest that habitat characteristics are more important than culvert-related factors in dictating rates of movement of this species.

Factors influencing Fundulus heteroclitus movement Our analysis of fish movement suggests that fragmentation of salt marsh leads to reduced connectivity for *Fundulus heteroclitus* in U.S. South Atlantic tidal creeks. *Fundulus heteroclitus* showed a higher probability of movement to sites with greater percentages of marsh-fringed shoreline and had limited or no movement to sites that lacked marsh. Similarly, Doak et al. (1992) concluded that the disruption of dispersal ability by nekton is a consequence of habitat fragmentation. There is also evidence from our data that water depth affects rates of movement of this dominant tidal creek species despite the fact that the two sites on either side of each crossing had adequate water levels to hold *Fundulus heteroclitus* over all tidal levels. The effect of water depth was not as strong as percent marsh but we found a lower proportional recapture rate at the shallowest sites and also at the deepest sites. This suggests that anthropogenic activities that

result in scour as well as siltation may result in reduced movement rates of this important tidal creek species.

It is unlikely that adult *Fundulus heteroclitus* transit between marsh patches that have become disconnected by instream development. We found via tag/recapture sampling (unpublished data: Chapter 5) that (depending on creek) few or no tagged adult *Fundulus heteroclitus* were recaptured in preferred salt marsh habitats after having been tagged in nearby salt marsh habitats within their home range distance but disconnected from recapture sites due to anthropogenic fragmentation.

We did not find an effect of culvert characteristics on *Fundulus heteroclitus* movement. This contrasts with previous work on fish movement in freshwater creeks (Warren Jr. and Pardew 1998; Poplar-Jeffers et al. 2009) and a study of fish passage through culverts bisecting New England (U.S.) salt marshes (Eberhardt et al. 2011). Eberhardt et al. (2011) provided strong evidence for the effects of water current velocity through culverts and culvert size (cross sectional area/length) on *Fundulus heteroclitus* movement. However, the large range of culvert lengths (78.8 m) and current velocities (~ 1.5 m/sec) in that study relative to ours may have enabled those researchers to detect pronounced effects of these two factors on movement. Other studies researching movement of small-bodied fishes have concluded that increased water speeds from undersized ('flow-constricted') culverts can reduce movement rates (Warren Jr. and Pardew 1998; Eberhardt et al. 2011; Januchowski-Hartley et al. 2014). Water current speeds > 0.4 m/sec have been found to deter movements of freshwater fundulids (Warren Jr. and Pardew 1998). The crossing with the second highest average current speed (Atlantic Veneer) had the highest *Fundulus heteroclitus* movement rates but current speeds there were below the 0.4 m/sec threshold identified by Warren Jr.

and Pardew (1998) and below the highest current velocities (~ 1.5 m/sec) where Eberhardt et al. (2011) observed reduced passage rates of *Fundulus heteroclitus* in New England. The crossing with the highest velocity in this study (Wading) lacked movement of tagged fish, and was above the Warren Jr. and Pardew (1998) velocity threshold for fundulids. This potentially indicates that there is a threshold velocity above which *Fundulus heteroclitus* will not pass through culverts in this area, but it appears from our sampling and observations in this region of coastal North Carolina that the number of culverts with current velocities exceeding 0.4 m/sec is low. Given the lack of movement at the Wading Creek crossing, potentially due to high current velocities, this could affect the analysis (mask the effect) of habitat features important to the movement probability of this species.

Given that other regions of the U.S. South Atlantic coast (e.g., South Carolina and Georgia coastlines) have substantially greater semi-diurnal tidal amplitudes than coastal North Carolina (Wiegert and Freeman 1990), it is likely that culverts in tidal creeks in these other areas have current velocities that are more likely to exceed any passage thresholds for *Fundulus heteroclitus* and other small-bodied nekton species. However, we are not aware of any other studies from relatively macro-tidal areas of the U.S. South Atlantic coast that have measured current velocities through tidal creek culverts or the responses of nekton species to them.

To our knowledge, this is only the third study of fish movement past crossings in tidal creeks (Eberhardt et al. 2011; Bowron et al. 2011). Our study builds on this earlier research by examining not only crossing-level attributes but also sample site-level characteristics that could influence nekton movement due to the possibility of fish passage being a function of the nekton species under study, culvert characteristics, and also one or more site-level factors

operating over multiple spatial scales (Januchowski-Hartley et al. 2014). Bowron et al. (2011) found that culvert widening increased the relative abundance of *Fundulus heteroclitus* in a macro-tidal area in the Bay of Fundy and attributed that fish response to increased high tide wetted area rather than the characteristics of the single crossing that was researched in that study. In contrast, culverts do not appear to limit upstream high tide water coverage in the micro-tidal region of the U.S. South Atlantic coast where this study occurred (pers. obs.). Thus, road projects and instream development in this study are likely to affect attributes of the crossings themselves (depth, current, culvert length) and the quality of inter-tidal habitat (vegetated vs. non-vegetated) but not change the amount of high tide wetted area landward of the culvert that is available for foraging or refuge by nekton.

Culverts did indirectly affect movement probability due to scouring (deepening) of soft-bottomed creek channels at crossings we studied. Inappropriately sized or shaped culverts can scour soft-bottom stream channels and adjacent vegetated habitats (Abt et al. 1984). This altered probability of movement by *Fundulus heteroclitus* past crossings we studied could be due to a lack of preferred habitat at these deeper sites, intentional avoidance of increased risk of predation at these anthropogenically-deepened sites (Ruiz et al. 1993), predation mortality, or a combination of these factors. *Fundulus heteroclitus* is known to prefer shallow water and intertidal salt marsh habitats (Able and Hagan 2003; Allen et al. 2007; Rudershausen et al. 2016) over deepwater habitats within the same marsh mosaic (Halpin 1997) but adults appear to take a risk-averse movement strategy to avoid stranding over very shallow depths (Rudershausen et al. 2014).

We considered the number of trials (N in the binomial distribution) to be only those instances when fish of a unique tag color and tagging location on the body were first

recaptured during a sampling event. For each sampling event, N constituted the sum of recaptured fish of that tag color and body location at both the upstream and downstream sample sites. Because the data on movement of *Fundulus heteroclitus* past crossings was restricted to sample events with a non-zero number of recaptures, the number of data points (trials) is limited for some crossings (< 10) despite intensive trapping and tagging efforts. High variability in biological response data is common in dynamic ecosystems such as salt marshes and necessitates high spatial replication to detect an ecological effect (Lee et al. 2006). Further work on this topic may reveal other factors important to the movement of *Fundulus heteroclitus* past crossings. Additionally, research into the ability of other important estuarine nekton species (e.g., *Leiostomus xanthurus*) to pass culvert crossings in U.S. South Atlantic tidal creeks is warranted.

Conclusions Over the range of culvert characteristics examined in this study we found that two sites in close proximity to each other will possess similar communities as long as their biological and physical habitats are similar, regardless of the characteristics of the culvert that separates them. The results from this study show that common anthropogenic impacts in the U.S. South Atlantic coastal zone – marsh fragmentation, shoreline armoring, and increased water depths from instream development – will affect nekton species composition and movement more than culverts by themselves, within the range of culvert characteristics included in this study.

It is forecasted that anthropogenic activities in tidal creek watersheds and intertidal zones will further fragment salt marsh habitats along U.S. coastlines (Kennish 2001; Mattheus et al. 2010; Gittman et al. 2015). For example, it is predicted that the percentage of armored shoreline will double by the year 2100 (Gittman et al. 2015). Pressure from ongoing

development heightens the importance of managing estuarine habitats to maintain connectivity among patches (Meynecke et al. 2008).

In order to lessen the impacts of development on marsh-resident nekton, natural resource managers would be well served to prioritize measures that preserve or restore salt marsh connectivity, reduce the rate of installation of armored shoreline by expanding the ‘living shorelines’ approach (Gittman et al. 2016), and consider novel culvert designs (Wargo and Weisman 2006) to help reduce scour in low-energy tidal creeks. Since culverts are often replaced and upgraded as part of road maintenance projects (Kemp and O’Hanley 2010; Januchowski-Hartley et al. 2013), coastal planners and transportation agencies in this region will have ongoing opportunities to restore salt marsh connectivity and improve fish passage as new roadworks projects arise.

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Table 3.1. Habitat and anthropogenic characteristics of ten crossings in first-order tidal creeks in coastal North Carolina sampled for nekton communities and movement of *Fundulus heteroclitus* in 2015-16. Ebb and flood-tide current speeds as well as water depths ('depth') were measured at mid-tide. Site types above and below each crossing were classified as: 1) lacking a culvert and having no impact (reference), 2) having a culvert next to them but otherwise having no impact (non-impacted) and 3) having a culvert next to them and impacted by development (impacted). The letter by each crossing name denotes the corresponding panel in Figure 3.1.

Crossing name (abbreviation)	Site type: above	Site type: below	Length (m)	Culvert pipe or channel cross-sectional area (m ²)	Depth upstream sample site (m)	Depth downstream sample site (m)	Ebb current speed (m/sec)	Flood current speed (m/sec)
Porters (A)	reference	reference	30	1.8	0.50	0.68	0.27	0.12
Atlantic Veneer (B)	non-impacted	non-impacted	13	0.8	0.40	0.58	0.23	0.34
Town (C)	non-impacted	non-impacted	28	10.2	0.39	0.37	0.13	0.10
Bridges (D)	non-impacted	non-impacted	46	2.4	0.20	0.40	0.01	0.01
Goose (E)	non-impacted	impacted	29	2.3	0.70	1.20	0.06	0.04
Wading (F)	impacted	non-impacted	11	1.6	0.90	1.00	0.73	0.46
Pelletier East (G)	non-impacted	impacted	36	2.4	0.40	0.78	0.47	0.10
Pelletier North (H)	non-impacted	impacted	38	1.7	0.23	1.68	0.04	0.09
Pelletier West (I)	non-impacted	impacted	30	2.5	0.70	0.84	0.20	0.07
Spooners (J)	non-impacted	impacted	19	4.5	0.79	0.90	0.38	0.07

Table 3.2. Results of analysis of similarities (ANOSIM) testing for pairwise differences in nekton communities among three types of sites in North Carolina tidal creeks. Site types were classified as: 1) lacking a culvert and having no impact (reference), 2) having a culvert next to them but otherwise having no impact (non-impacted) and 3) having a culvert next to them and impacted by development (impacted). Sites were sampled with wire mesh minnow traps on both sides of ten crossings in first-order tidal creeks in coastal North Carolina in 2015-16. ANOSIM *R* values > 0.2 were considered to indicate community differences. Results from similarity percentages (SIMPER) analysis show the species making the greatest proportional contribution to nekton community differences for each significant ANOSIM result.

Site pairing	ANOSIM		SIMPER	
	<i>R</i>	p	Taxa	proportion
reference vs. non-impacted	0.075	0.046	<i>Fundulus heteroclitus</i>	0.715
reference vs. impacted	0.324	0.001	<i>Fundulus heteroclitus</i>	0.559
non-impacted vs. impacted	0.382	0.001	<i>Fundulus heteroclitus</i>	0.551

Table 3.3. Bayesian probability values (p), Bayes factors (K) and the 2.5, median and 97.5 credible intervals of partial regression coefficients from fitting each of eight binomially distributed generalized linear mixed models to data on movement of *Fundulus heteroclitus* through road and reference crossings in tidal creeks in coastal North Carolina. Models are listed in descending order of their K values. See *Methods* for a description of covariates.

Model	Covariate	p	K	2.5	Median	97.5
1	Percent marsh edge	0.300	232.33	0.010	0.030	0.050
	Current velocity			9.439	36.048	100.940
	Current velocity ²			-259.873	-75.761	-13.865
	Percent marsh edge*current velocity ²			-0.948	-0.293	0.717
2	Water depth	0.328	107.87	2.981	21.818	42.882
	Water depth ²			-39.149	-22.526	-6.806
	Current velocity			-43.721	31.005	114.227
	Current velocity ²			-283.964	-70.858	101.131
	Water depth ² *current velocity ²			-189.497	-15.210	137.489
3	Percent marsh edge	0.321	24.80	0.012	0.049	0.123
	Crossing length			-1.606	0.313	2.760
	Crossing length ²			-0.050	-0.006	0.031
	Percent marsh edge*crossing length ²			0.000	0.001	0.002
4	Water depth	0.391	17.57	2.809	17.645	35.250
	Water depth ²			-33.443	-18.464	-6.611
	Crossing length			-0.861	0.252	2.095
	Crossing length ²			-0.037	-0.006	0.016
	Water depth ² *crossing length ²			-0.010	-0.003	0.004
5	Current velocity	0.291	9.92	-20.749	40.298	169.178
	Current velocity ²			-420.672	-93.286	48.219
6	Percent marsh edge	0.349	6.91	0.007	0.025	0.046
7	Crossing length	0.297	2.33	-1.269	0.074	1.778
	Crossing length ²			-0.032	-0.002	0.023
8	Water depth	0.443	0.67	2.114	15.267	34.196
	Water depth ²			-31.333	-15.108	-4.771

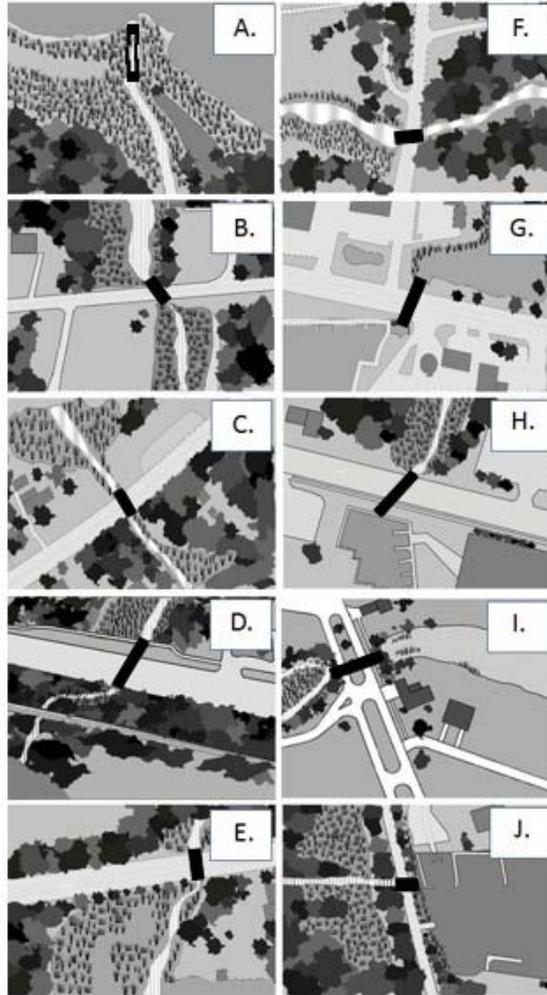


Figure 3.1. ‘Birds-eye view’ sketches of ten crossings in first-order tidal creeks in coastal North Carolina studied for nekton communities and movement rates of *Fundulus heteroclitus* in 2015-16. The open rectangle in Panel A denotes the length of the reference crossing, which lacked a culvert. The filled black rectangles in the other panels denote crossings with culverts. Sample sites on each side of the crossings in Panels A-D were considered non-impacted while one sample site at each of the crossings in Panels E-J was considered impacted by instream development. Road surfaces are represented by the lightest gray shade, upland by the next lightest gray, buildings by gray squares, standing water by darker gray, sub-tidal creek channels by white with black hatching, and salt marsh by gray with black tussocks. Blotched multiple grayscale shading represents tree cover.

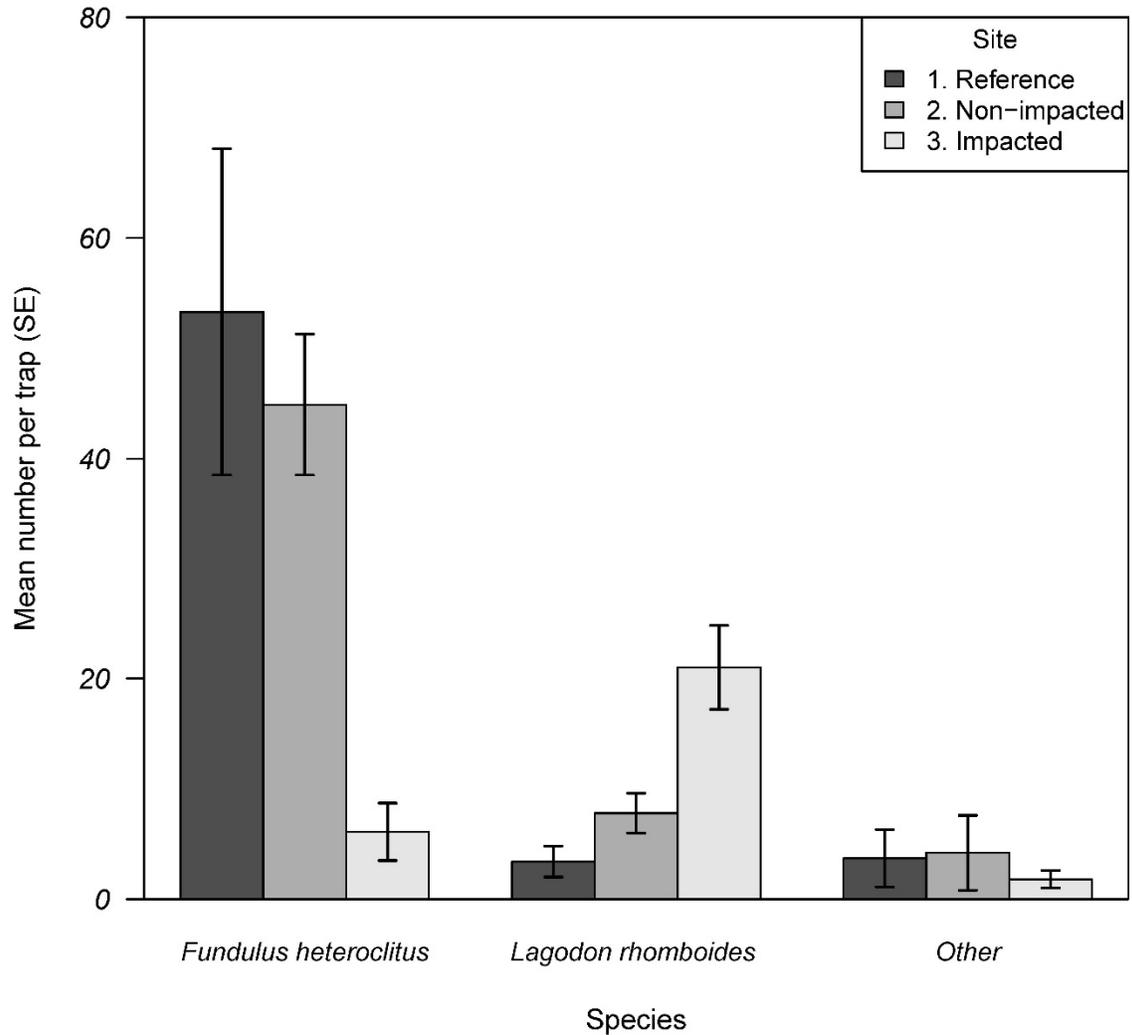


Figure 3.2. Bar graphs depicting the mean abundance (SE) (y axis) of three taxa groupings of nekton collected by wire mesh minnow traps (x axis) at three types of sites in tidal creeks in North Carolina. The site types were those: 1) lacking a culvert and having no impact (reference = no culvert), 2) having a culvert next to them but otherwise having no impact (non-impacted) and 3) having a culvert next to them and impacted by development (impacted).

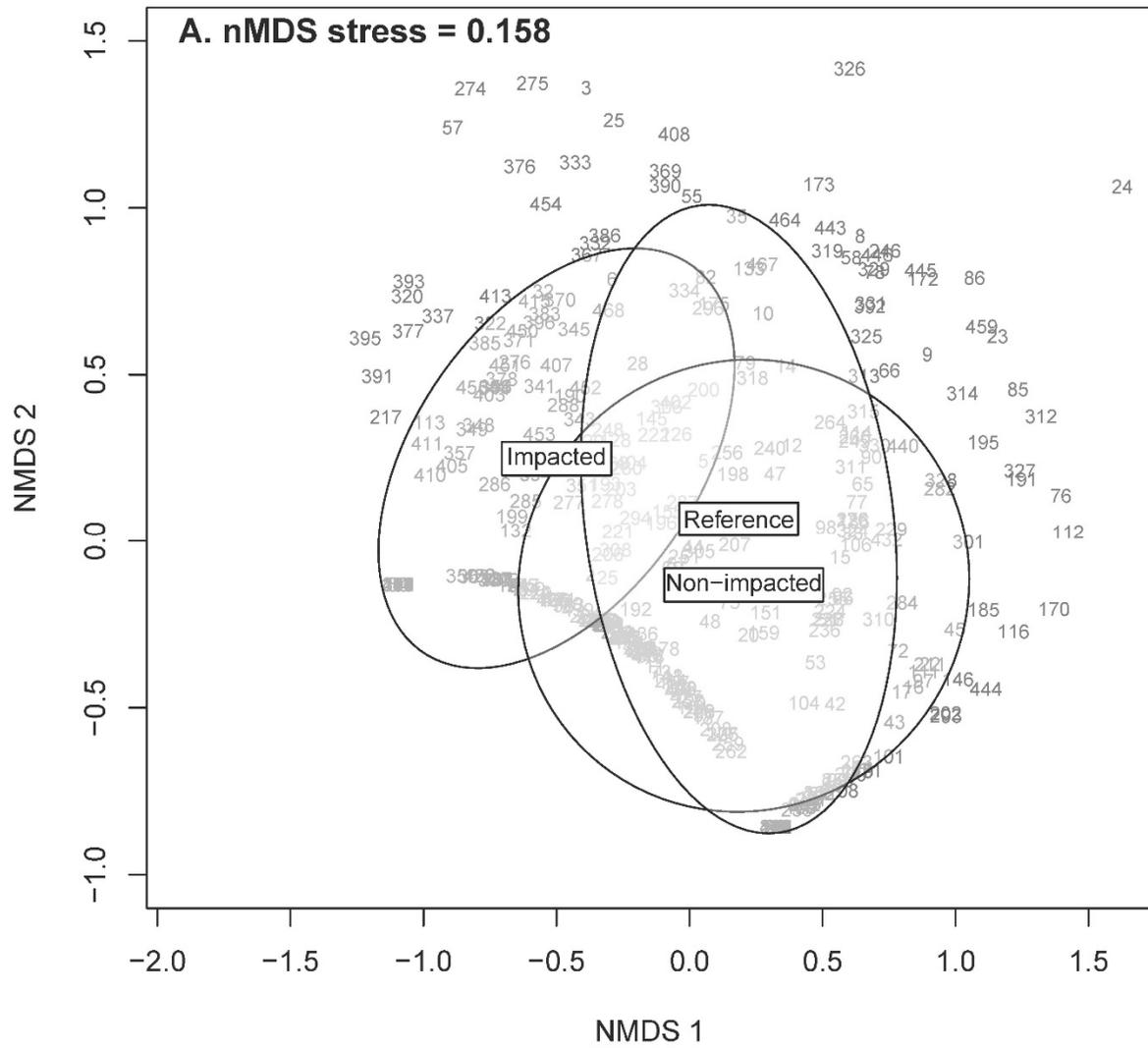


Figure 3.3. Non-metric multidimensional scaling ordination of minnow trap samples collected from three site types in North Carolina tidal creeks. Site types were: 1) lacking a culvert and no impact (reference), 2) having a culvert next to them but otherwise no impact (non-impacted) and 3) having a culvert next to them and impacted by development (impacted). Ordination stress was 0.158. Samples from each trap deployment with a non-zero catch are shown by small gray numbers in each panel. Panel A: Centroids (label locations) and standard deviation ellipses of communities for each site type. Panel B: Direction and strength (length of arrow) of two continuous habitat/anthropogenic factors (water depth at the site ('SiteDepth') and distance to the nearest marsh patch ('DistanceNearestMarsh')) and the centroid of each class (1 = presence, 0 = absence) of a binary variable ('Bulkheading') with the greatest correlation with samples dissimilarities. Panel C: Direction and strength of each taxon of fish and invertebrates with the greatest rank correlation with dissimilarities among samples. The x and y axes are identical among panels.

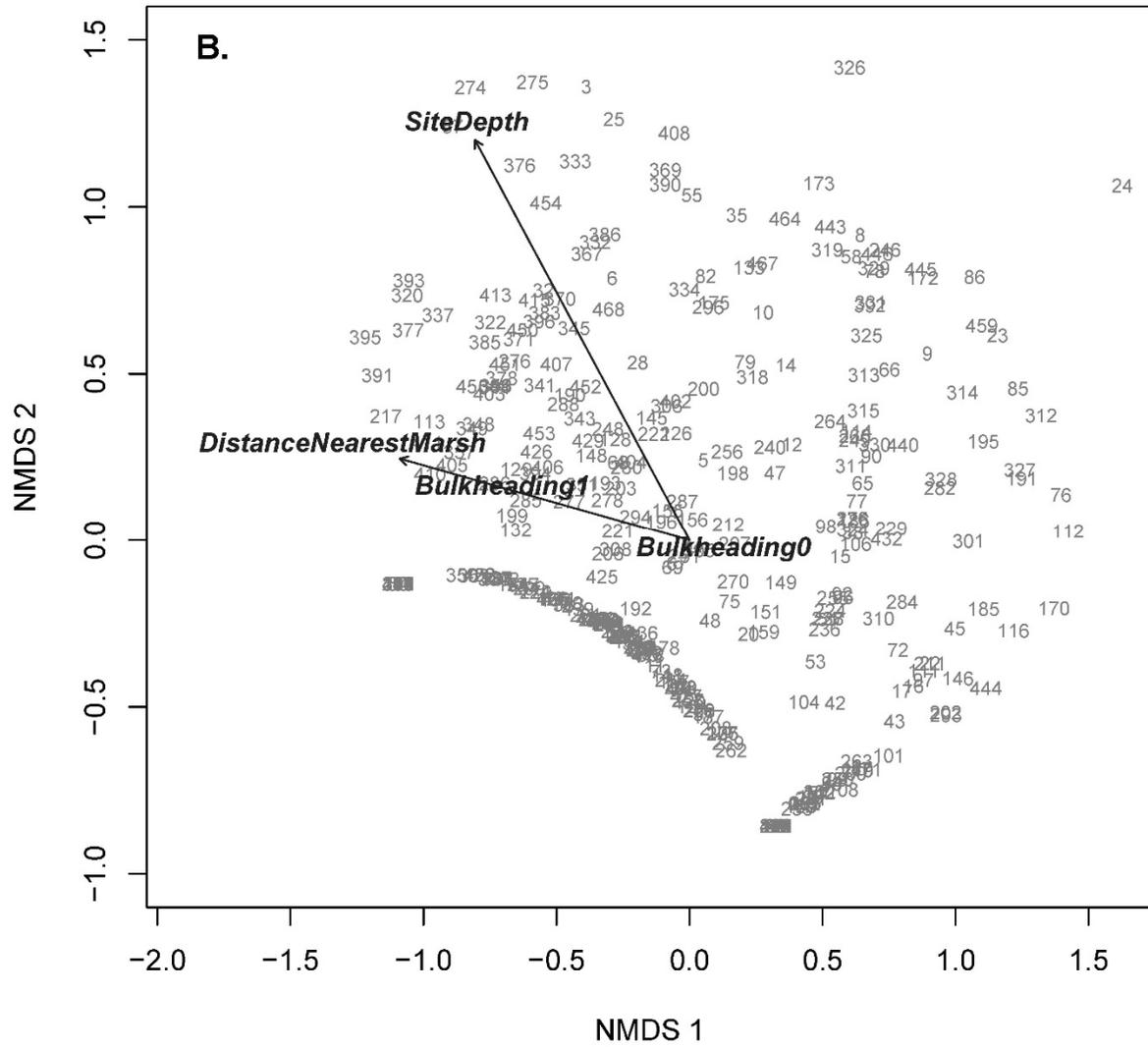


Figure 3.3 (con't)

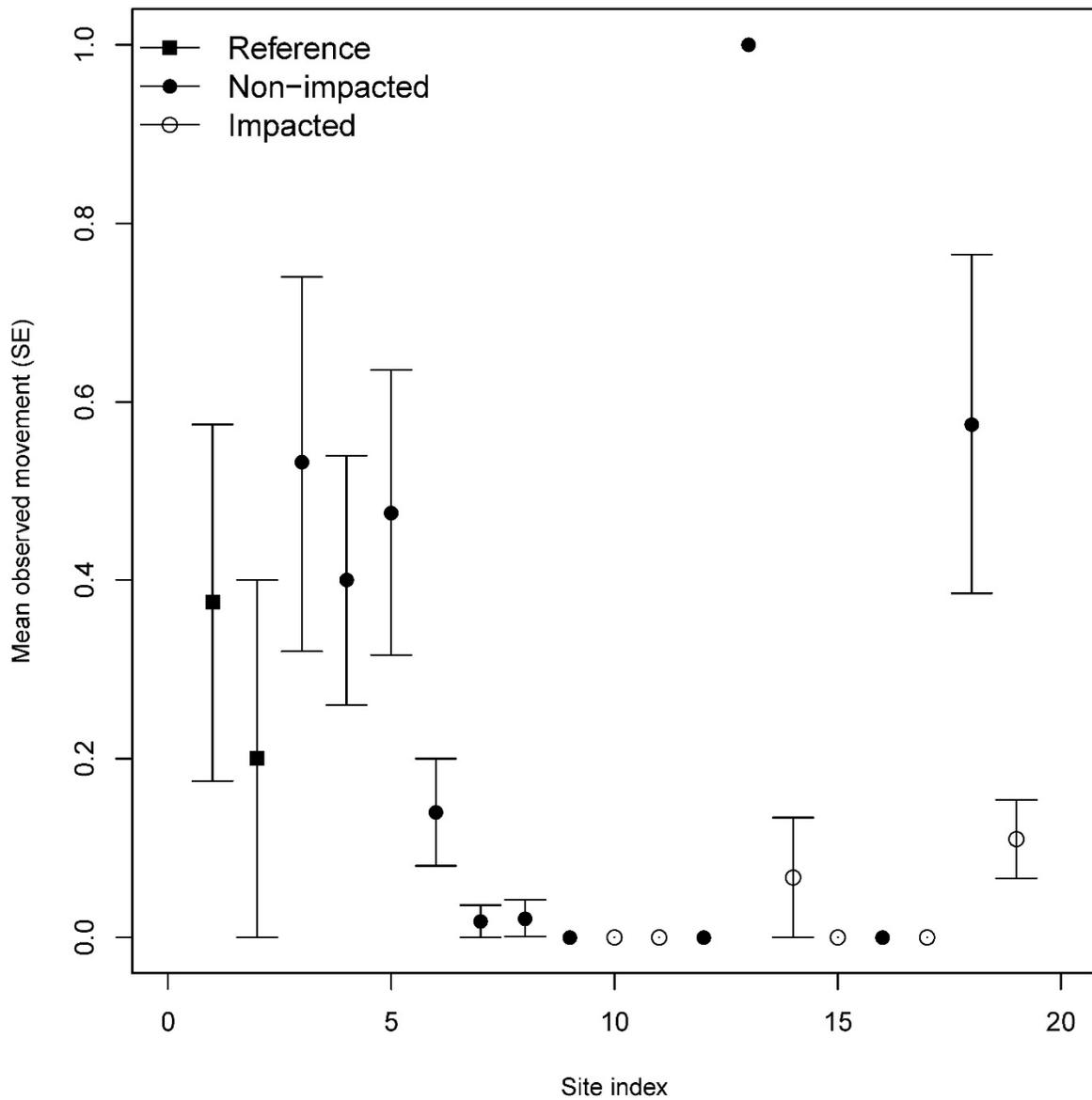


Figure 3.4. Mean observed proportional movement (\pm SE) of *Fundulus heteroclitus* past tidal creek crossings in coastal North Carolina (y axis) for each of 19 sites where recaptured fish were collected. Sites across the x axis are listed in the same order as Table 3.1; the exception is that no recaptured fish moved from the downstream site to the upstream site at Pelletier North Creek (no plot data). The three different symbols are specific to each of the three site types: reference, non-impacted, and impacted; see *Methods* for a description of the site types.

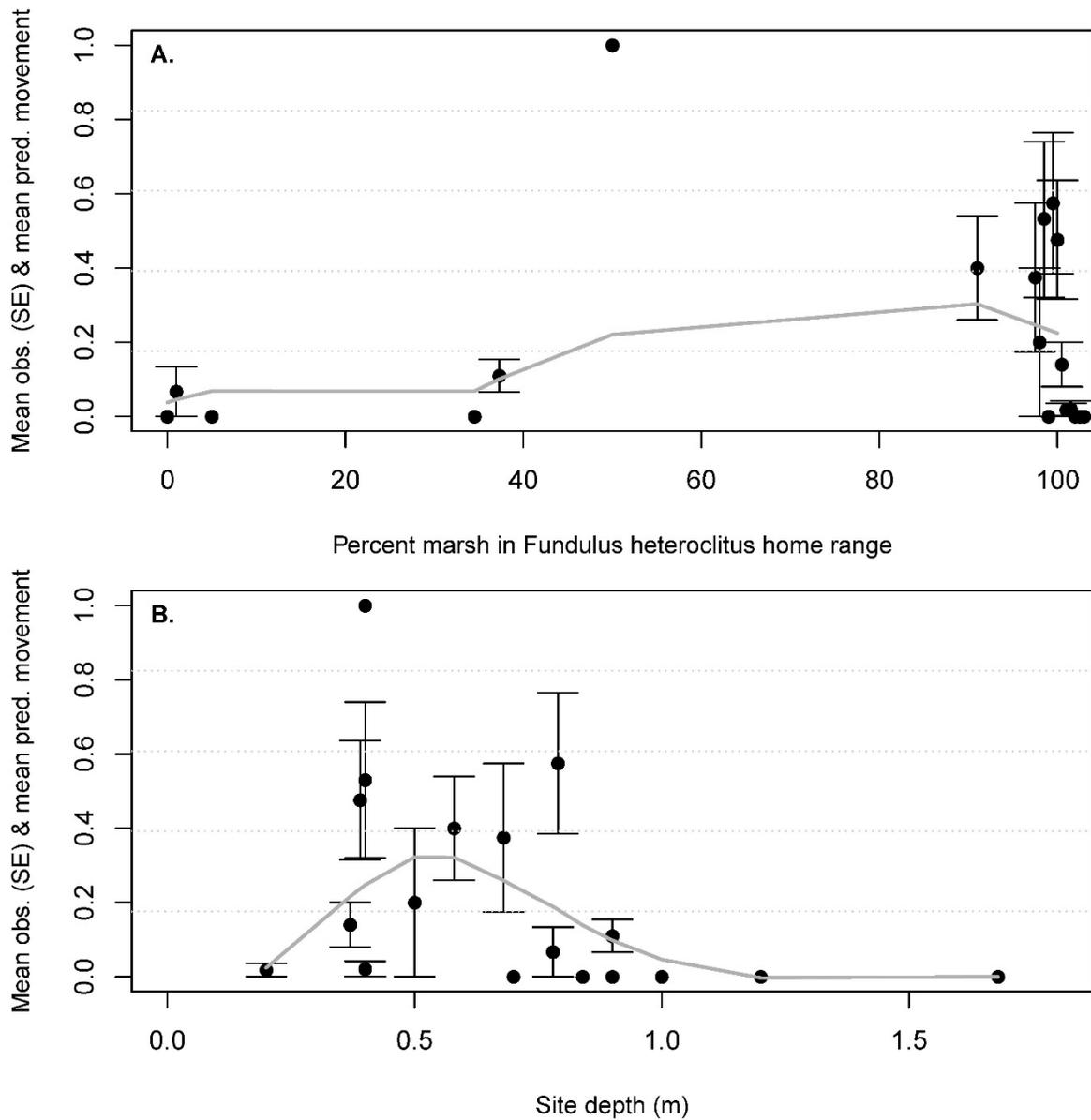


Figure 3.5. Mean observed proportional movement (\pm SE) (black symbols and vertical error bars) and predicted proportional movement (gray lines) of *Fundulus heteroclitus* past tidal creek crossings in coastal North Carolina (y axis) as a function of percent marsh-fringed shoreline within the species home range at sites to where individuals moved (Panel A: x axis) and water depth at sites to where individuals moved (Panel B: x axis). Predictions are from the two generalized linear models that best fitted the data (see values for Bayes factors, Table 3.3). The predicted line in each panel was plotted using a smoothing parameter whose value was set to 0.5.

CHAPTER 4. ESTIMATING MOVEMENT AND SURVIVAL RATES OF A SMALL SALTWATER FISH USING AUTONOMOUS ANTENNA RECEIVER ARRAYS AND PASSIVE INTEGRATED TRANSPONDER TAGS

Paul J. Rudershausen, Jeffrey A. Buckel, Todd Dubreuil, Matthew J. O'Donnell, Joseph E. Hightower, Stephen J. Poland, and Benjamin H. Letcher

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ABSTRACT

We evaluated the performance of small (12.5 mm) passive integrated transponder (PIT) tags and custom detection antennas for obtaining fine-scale movement and demographic data of *Fundulus heteroclitus* in a salt marsh creek. Apparent survival and detection probability were estimated using a Cormack Jolly Seber (CJS) model fitted to detection data collected by an array of three vertical antennas from November 2010 to March 2011 and by a single horizontal antenna from April to August 2011. Fish movement was monitored during the period when the array of vertical antennas was used. Antenna performance was examined *in situ* using tags placed in wooden dowels (drones) and in live *Fundulus heteroclitus*. Forty-two out of 44 tagged fish were resighted over the nine month monitoring period. The *in situ* detection probabilities of the drone and live fish were high (~ 80 - 100%) when the ambient water depth was less than ~ 0.8 m. Upstream and downstream movement of *Fundulus heteroclitus* was related to water depth and direction of tidal current in a way that maximized the time over which *Fundulus heteroclitus* utilized the intertidal vegetated marsh. Apparent survival was lower during periods of colder water temperatures in December 2010 and early January 2011 (median estimate of daily apparent survival = 0.979) than during other periods

of the study (median estimate of daily apparent survival = 0.992). During the late fall and winter, water temperature had a positive effect on the CJS detection probability of tagged *Fundulus heteroclitus*, likely due to greater fish activity over warmer occasions. During the spring and summer, this pattern reversed, possibly due to *Fundulus heteroclitus* having reduced activity over the hottest occasions. This study demonstrates the utility of small PIT tags and continuously operating autonomous detection systems to track fish at fine temporal scales in saltwater and improve estimates of demographic parameters in salt marsh creeks that are difficult or impractical to sample with active gears.

INTRODUCTION

Salt marshes are widely studied ecosystems that are important habitats for biological production along the United States east coast (Seabrook 2012). These systems provide ecological services (e.g., habitat for secondary and tertiary consumers, carbon storage, and water filtration) that can be hindered by human encroachment (Dame et al. 2000). Salt marshes offer an opportunity to examine specific questions such as the behavioral mechanisms of habitat selection over fine time scales due to variation in habitat profitability as a function of tidal cycles (Craig and Crowder 2002). Studies of salt marsh fish production, demographics, habitat use, and movement are often compromised when using traditional gears (e.g., trawls and seines) due to the inefficiency of using them to collect data over repeated sampling in soft-bottom tidal creeks (Kneib 1997).

Many species of estuarine resident and transient fishes along the U.S. South Atlantic coast utilize salt marsh habitats for feeding and for refuge from predation (Kneib and Wagner 1994; Kneib 2003; Bretsch and Allen 2006). However, current knowledge of the use of intertidal marsh habitats by fish is based largely on ebb-tide collections of groups of animals

(Kneib 2003; Bretsch and Allen 2006). Such batch collections provide little temporally fine-scale (e.g., hourly) information about the extent or duration of habitat use by fishes and crustaceans in intertidal marshes (Kneib and Wagner 1994). Additionally, traditional gears do not allow precise estimation of demographic parameters due to the infrequency of recaptures of tagged individuals in such studies (Kneib and Craig 2001; Hewitt et al. 2010; Camp et al. 2011).

Passive integrated transponder (PIT) tags are a tool by which biota in salt marsh systems can be resighted with higher resolution and less effort than traditional techniques (e.g., trapping, seining, and weiring). While widely used in freshwater ecosystems, PIT tags have been relatively little used in saltwater habitats. The greater conductivity of saltwater compared to freshwater increases the attenuation of electromagnetic wave propagation and hence ability of antennas to detect full duplex (FDX) PIT tags carried by animals in these environments (e.g., Bogie 1972; Bass et al. 2012).

In several previous studies the higher resighting rates of PIT tags have resulted in greater precision about estimates of movement and demographic rates than using traditional recapture techniques in freshwater (Prentice et al. 1990; Hewitt et al. 2010) and saltwater environments (Adams et al. 2011). Large (23 mm) half duplex (HDX) PIT tags have been used to determine patterns of salt water fish spawning (McCormick and Smith 2004), survival (Adams et al. 2006), and movement (Adams et al. 2006; Meynecke et al. 2008; Adams et al. 2011) as the detectability of this type of PIT tag is not hindered by salinity (Castro-Santos et al. 1996). Relatively new, smaller FDX PIT tags (available in lengths down to 8.4 mm) can be used to mark smaller-bodied fishes (see Hering et al. 2010) than

what could be tagged with the smallest HDX tag size (23 mm) available when this study commenced.

Fundulus heteroclitus is the most abundant resident fish species inhabiting salt marsh creeks along the United States east coast (Kneib 1986; Kneib 1997; Able and Fahay 1998). Given its small home range (Lotrich 1975; Meredith and Lotrich 1979; Teo and Able 2003) and high site fidelity (Sweeney et al. 1998; Teo and Able 2003; Skinner et al. 2005), it is an ideal species through which to examine the utility of FDX PIT tags in salt marsh habitats. *Fundulus heteroclitus* can be autonomously sampled with PIT tags to improve on published estimates of movement (Kneib and Wagner 1994; Teo and Able 2003; Bretsch and Allen 2006) and survival (Meredith and Lotrich 1979) that have resulted from batch collections of multiple species or non-electronic tagging. The marking technique and detection devices used in this study are also useful for studying a wide range of ecological questions related to salt marsh nekton.

Our objectives in this study were to evaluate the performance of small (12.5 mm) FDX PIT tags and custom antennas in a salt marsh creek and apply these tagging and detection technologies to obtain estimates of movement and survival of a dominant salt marsh fish species via autonomous monitoring. To our knowledge, this is the first study to estimate survival of a saltwater fish species with 12.5 mm PIT tags. Thus, vetting the use of small PIT tags opens a range of possible ecological and demographic studies that can be undertaken on small-bodied nekton in saltwater habitats.

METHODS

Study Site The study site was Porters Creek, a 600-m long first-order intertidal polyhaline creek in the Newport River Estuary, North Carolina (Figure 4.1). The lower 500 m of this

creek are unrestricted and fringed by vegetated intertidal salt marsh dominated by salt marsh cordgrass *Spartina alterniflora* (Loisel) while the upper 100 m are upstream of a culvert road crossing and fringed by forest. Porters Creek has tidal amplitudes of ~1.0 m during spring tides and 0.7 m during neap tides with amplitudes affected primarily by astronomical forcing and secondarily by wind speed, direction, and duration (Kirby-Smith and Costlow 1989). The fringing marsh in Porters Creek is flooded for ~ 3.5 hours over each semidiurnal tidal cycle. Flooding of marsh vegetation occurs at a depth (where the PIT tag antenna array was located) of 0.5 m. Current speeds in the channel of Porters Creek during that portion of the tidal cycle when the marsh platform is drained are ~ 0.4 m/sec over ebb tides and 0.2 m/sec over flood tides where the antennas were located. Salinities taken intermittently in Porters Creek throughout the study ranged from 5 to 39 psu (mean = 30 psu).

Fish collection and marking Fish were collected on 8 November 2010 within 50 m of the detection antennas using Gee-style minnow traps made of 6.4 mm square wire mesh. We tagged 44 *Fundulus heteroclitus* ranging from 50 to 94 mm total length (1.5 – 13.1 g). We anesthetized fish with tricaine methanesulfonate (125 g/l of seawater) prior to implanting the tag in the peritoneal cavity. We implanted FDX PIT tags (12.5 mm, 0.1 g) (Biomark, Inc., Boise, ID) with a frequency of 134.2 kHz by making a small (~ 1 mm) incision on the ventral side of the fish posterior of the pelvic girdle. We used FDX instead of HDX tags because HDX tags were not available in small sizes (≤ 12.5 mm) when this study commenced. Each tagged fish was then placed in a recovery tank of ambient seawater and later released in the vicinity of the capture location once swimming under its own power. A separate laboratory study determined that the overall PIT tagging success (probability of retaining a tag and

surviving the surgery) in *Fundulus heteroclitus* (41 to 70 mm) was 87%; all mortality and tag shedding occurred within the first 30 d of the 163 d experiment (Brewer et al. 2016).

Tag detection equipment From 8 November 2010 through 3 March 2011 we used an array of three rectangular antennas (a ‘vertical array’) to detect PIT-tagged *Fundulus heteroclitus* moving past a fixed point in the study creek. Each antenna was custom-made from nine wraps of 10 AWG 1100/40 polyvinyl chloride (PVC) coated Type II Litz wire (New England Wire Co., Lisbon, NH) encased with controlled spacing in 15-cm diameter schedule-40 PVC pipe. The internal dimensions of each antenna defined the rectangular opening through which fish could pass during movement into or out of the creek. Each antenna had an internal height of 0.7 m (space between the two horizontal PVC pipes). The downstream and upstream antennas in the array (numbers 1 and 3, respectively) had internal widths of 1.75 m while the middle antenna’s internal width (number 2) was 2.25 m. Antennas were positioned 4 m apart; at this distance each antenna had its own detection field. Both the vertical antennas and the horizontal antenna (described below) were secured to- and rested on the substrate with sand screws and ratchet straps.

The three antennas were oriented perpendicularly to the channel and placed 50 m upstream from the creek mouth (Figure 4.1 and 4.2A). This location is a transition area at mean low tide between a rivulet of water that persists in the non-vegetated channel above the array and standing water that persists over the width of Porters Creek during all tidal cycles below the array. To maximize path efficiency (Zydlewski et al. 2006), plastic weir material (6.4 mm square mesh) was affixed to the top and sides of the upstream and downstream antennas; the side weir material was extended from these two antennas to the high-tide line.

The vertical antenna array and weir material were removed from the creek on 3 March 2011 and replaced with a single antenna on 14 April 2011 that was horizontal (flat) with respect to the creek bottom and placed in the same location as the middle antenna of the vertical array (Figure 4.2B). The horizontal antenna was constructed of nine wraps of 10 AWG 1100/40 PVC coated Litz wire embedded in 20.3 cm diameter schedule 40 PVC. However, no weir material was used with the horizontal antenna. The internal dimensions of the horizontal antenna were identical to vertical antennas 1 and 3 (0.75 x 1.75 m). The switch to a single horizontal antenna was required to permit seasonal use of the study creek by paddle boaters. Each antenna (during both the vertical and horizontal antenna periods) was connected via RG-8 coaxial cable (Belden, Richmond, IN) to a 24 volt FS-1001-M multiplexing receiver (Destron Fearing, St. Paul, MN). The receiver was powered by two pairs of 12 volt DC batteries connected in series to create two 24 volt batteries. A custom-made battery switcher alternately switched charging of each pair of batteries with a charger (Model PS 2408 charger; Interacter Inc., Meridian, CT) connected to 120 volt AC electrical power. The receiver was connected to a cellular modem (Raven XT V2221; Sierra Wireless, Carlsbad, CA). The modem provided remote access to the receiver and facilitated automatic daily downloads of text files containing tag codes, dates, and times when tagged fish were detected as well as receiver diagnostics such as electrical current and radio frequency (RF) noise readings (external disturbance to an electrical circuit) of each antenna. The receiver, batteries, battery switcher, recharger and modem were stored in an electrical box affixed to a sheltered kiosk. There were occasions during the monitoring period (Table 4.1) when the multiplexing receiver was not operational. During these occasions a Destron Fearing 24 V

FS-1001A receiver was used. Unlike the multiplexer, the FS-1001A does not provide date and time of each detection; detections by the FS-1001A were assigned a date at the midpoint between manual downloads of data (Table 4.1). PIT tag readers are incapable of determining the specific vertical or horizontal location of a detection within the plane of an antenna.

We collected data on water temperature and water depth in order to evaluate their relationship with the Cormack Jolly Seber (CJS) model parameter, detection probability (see below). We placed a Hobo 20 Titanium logger (Onset Corp., Bourne, MA) next to Antenna 2; this logger recorded hourly temperature (0.1 °C) and water depth (0.1 m) throughout the study. The hourly water depth closest in time to each tag detection was used to evaluate the effects of depth on number of detections by each antenna.

Evaluation of antenna performance and probability of detecting PIT tags Using linear regression models we examined the effect of water depth on electrical current (higher current = higher probability of detection) for each vertical antenna from 8 November 2010 through 3 March 2011. Fish detections were examined on plots of electrical current vs. water depth to determine if reductions in the number of detections with greater water depth resulted from poor antenna performance or fish behavior. If the number of detections decreased but antenna current remained sufficiently high for detecting fish ($> \sim 1$ ampere), this would suggest that fish behavior was responsible for the lack of detections rather than antenna performance. Analysis of covariance (ANCOVA) of electrical current (dependent variable) and depth (covariate) was used to determine if the amount of electrical current varied by antenna number (factor). Values for electrical current were natural logarithm (ln)-transformed to linearize their relationship with water depth.

The probability of detecting a PIT tag *in situ* was estimated using both a drone tag and live *Fundulus heteroclitus*. Drone tag testing was conducted to determine how water depth and tag position influenced the probability of tag detection by the custom-made antennas. The drone consisted of a 12.5 mm FDX PIT tag embedded in a wooden dowel. We passed the drone through a 0.75 x 1.75 m vertical antenna in the field at a water temperature of 26°C and a salinity of 25 psu. This salinity is similar to the average salinity in Porters Creek (~ 30 psu). Factors examined were those known to influence FDX PIT tag detection included water depth (depth), the height that the tag was passed relative to creek bottom (tag height), and the horizontal location within the antenna perimeter where the drone tag was passed (Horton et al. 2007; Hering et al. 2010; Bass et al. 2012). We selected discrete water depths (0.2, 0.4, 0.6, 0.8, 1.0, and 1.1 m), tag heights (0, 0.2, 0.4, 0.6, 0.8, and 1.0 m), and horizontal locations (0, 0.25, 0.5, and 0.75 m from each vertical side of antenna) over which to test the drone. Each pass of the drone through the antenna lasted roughly one second. We performed one trial (pass of the drone) for each combination of water depth and tag height because pilot testing of PIT tags in salt water revealed that the outcome of detection trials did not change for any one combination of abiotic conditions and tag position inside the perimeter of the antenna.

Binomial drone tag detection data were fitted to water depth, tag height, horizontal location and their interactions using generalized linear models (GLMs). Model performance was evaluated with quasi-Akaike Information Criteria (QAICc) owing to potential over-dispersion of the data (values of the variation inflation factor frequently greater than 1). We computed a Δ QAICc value for each model, representing the difference between that QAICc

value and the minimum for the model set (QAICc_{min}). Models within 2 Δ QAICc units of QAICc_{min} were regarded as having substantial support (Burnham and Anderson 2002). Proportional support for each model was estimated using Akaike weights (w_i ; Burnham and Anderson 2002).

The *in situ* probability of detecting a tagged fish was estimated utilizing fish detection data collected during the study period when the vertical array was used. *In situ* detection probability is determined when a live fish or drone is known to be present in the antenna field and represents the performance of a single antenna. In contrast, CJS detection probability includes both *in situ* detection probability of all the antennas in the array (the probability of detecting a fish if it is present) and the probability that the fish is present (available) for resighting. Unlike detection probability estimated in the CJS model (below), *in situ* detection probability does not pool detections across all the antennas when a study uses a multiple-antenna array.

In situ detection probability was determined for individual *Fundulus heteroclitus* detected by at least Antennas 1 and 3 within a 10 minute period. This provided a group of fish known to have passed through Antenna 2. For those individuals, detection efficiency was then estimated as the number of times a tagged fish was detected by Antenna 2 (i.e., all three antennas in the 10 minute period) divided by the sum of detections on “all three antennas” and “Antennas 1 and 3 only”. The relationship between *in situ* detection probability and water depth was then modeled with logistic regression.

Using PIT tags to determine movement patterns Direction of movement of *Fundulus heteroclitus* was estimated from detection data collected during the study period when the

vertical array was used. We defined a valid movement as detections by at least two antennas within a ten minute period, with the first and last detections in the direction of movement. This definition avoided the assignment of movement to tagged fish that were occupying the antenna area of the creek for extended periods of time.

We modeled direction of movement through the array with logistic regression by assigning codes of 1 and 0 to upstream and downstream movements, respectively. We developed models that incorporated factors believed to influence direction of movement for *Fundulus heteroclitus* (Butner and Brattstrom 1960; Lotrich 1975; Teo and Able 2003). These factors were hourly water depth (to the nearest 0.01 m) and tidal current (flood vs. ebb). Model building (with respect to interaction terms) and model evaluation used the same criteria as described for drone tag data.

Using PIT tags to estimate apparent survival using the Cormack Jolly Seber model Detection probability and apparent survival of tagged *Fundulus heteroclitus* were estimated using a hierarchical state-space formulation of the CJS model (Cormack 1964; Jolly 1965; Seber 1965; Royle 2008). The likelihood in this version of the CJS model includes a state process (whether a marked individual is alive at sample time t) and an observation process conditioned on state (whether individual i is observed given that it is alive at time t and in the study area). The CJS model assumes that: 1) capture (resighting) periods are instantaneous relative to the time between them; 2) resighted fish are a random sample from the population; 3) behaviors of tagged individuals are independent but all individuals have the same survival and resight probability; 4) tags are not lost or overlooked; 5) individuals are correctly identified, and; 6) any emigration from the study area is permanent. The study area was both

above and below the antenna arrays in Porters Creek. We modeled apparent survival (1-(mortality + emigration)) of fish due to the open study area and potential for permanent emigration. Given the small home range size (Lotrich 1975; Meredith and Lotrich 1979) and high site fidelity of this species (Sweeney et al. 1998; Teo and Able 2003; Skinner et al. 2005), permanent emigration appears unlikely.

Although fish were detected up until 4 October 2011 (Table 4.1), we fitted the CJS model to data collected over 167 occasions between 8 November 2010 and 15 August 2011 when detections were continuous (i.e., no long breaks between occasions when detections occurred). The model was implemented using a Bayesian approach within *OpenBUGS* software (version 3.2.1; Spiegelhalter et al. 2010). An occasion was defined as a biologically meaningful unit of time over which independent Bernoulli trials (presence/absence) are conducted on tagged individuals in order to estimate demographic rates (Royle 2008). We elected to define an occasion as one day (24 hours) because we felt that this was a sufficiently long enough period to detect a tagged fish moving by the array over a variety of water depths and tidal stages but a short enough period (high enough temporal resolution) that we could identify any changes in patterns of apparent survival with fluctuations in temperature. Some occasions were longer than one day due to equipment issues (Table 4.1). Because several occasions were longer than one day, a day vector (number of days per occasion) was used to estimate daily values of apparent survival in the likelihood portion of the model.

We developed a form of the CJS model that incorporated covariates believed to influence fish behavior and the likelihood of detection probability by each antenna array.

Based on plots of numbers of unique individuals detected by occasion, it appeared that occasion-specific variability in p was related to water temperature, water depth, and array design (the vertical array vs. the single horizontal antenna). Thus, we elected to fit versions of the CJS model to the individual ‘capture’ (detection) histories that estimated detection probability by occasion using logistic models (with water temperature and water depth as continuous covariates) specific to each antenna array type; in initial model runs, we eliminated covariates when their slope coefficients had 95% credible intervals containing zero. These initial model runs eliminated water depth as a covariate but retained water temperature during the periods over which both the vertical array and horizontal antenna were used. To increase the efficiency of the Markov Chain Monte Carlo (MCMC) sampler within *OpenBUGS* (McCarthy 2007), we centered the variable water temperature for each occasion internally within each model run.

In order to detect potential water temperature effects on apparent survival, we used *OpenBUGS* to estimate a daily value of apparent survival specific to each of two periods. These two periods were selected based on differences in water temperature patterns. Period 1 included two time intervals: from 8 November to 1 December 2010 and from 24 January 2011 to 15 August 2011; a preliminary model run found that the credible intervals about estimates of apparent survival overlapped between each of these time intervals. During these time intervals the water temperature was below 5°C on only one day and often within the range of optimal growth of the species (Garside and Morrison 1977). Period 2 was a late fall/early winter time interval between 2 December 2010 and 23 January 2011, when the water temperature dropped below 5°C on multiple days.

For the Bayesian analysis with *OpenBUGS*, we used uninformative prior probability distributions. A normal prior probability distribution with mean of zero and precision of 1×10^{-6} was given to each coefficient (intercept and slope) of the two logistic models of CJS detection probability. The prior for apparent survival over each of the two periods was a uniform distribution with minimum (0) and maximum (1) possible values of apparent survival. Three Markov chains (independent sample sets) began with a burn-in period of 10,000 iterations (discarded initial values not representative of a stationary distribution). A sufficient burn-in period was determined by examining for convergence of chains of initial values in the trace plots generated in *OpenBUGS*. We then generated 100,000 updates of the model with every 10th iteration saved (thin = 10). This number of updates was selected because changes to the median values of- and credible intervals about parameter estimates no longer occurred compared to lesser numbers of updates of the same model.

RESULTS

Evaluation of antenna performance and probability of detecting PIT tags A total of 20,703 individual detections (individual resightings by any antenna at any time) were made by the vertical antenna array from November 2010 to March 2011. The majority of detections by vertical antennas occurred when water depths were shallow; overall, ~85% of detections occurred at water depths less than ~ 0.5 m. The slopes of linear regressions relating ln-transformed values of electrical current to water depth were significantly negative for each antenna ($p < 0.001$) (adjusted r^2 values of 0.867, 0.836 and 0.864 for Antennas 1, 2, and 3, respectively); diagnostic plots did not reveal multi-collinearity, non-normality, or non-constant error variance in the three regression models. There was a significant interaction

between water depth and antenna in the ANCOVA model ($p < 0.001$); Antenna 2 had lower electrical current at shallow water depths than Antennas 1 or 3 (Figure 4.3).

Water depth, tag height, and horizontal location within the antenna, and the interaction between water depth and tag height explained a large amount of variability in the antenna's ability to detect a drone tag *in situ* and were included in the most parsimonious model (Nagelkerke $r^2 = 0.875$; Table 4.2). Increasing water depth negatively affected detection probability for the drone while increasing tag height positively affected detection probability. Passes of the drone at horizontal distances of 0.25, 0.5, and 0.75 m had a negative effect on detection probability relative to 0 m. At a horizontal distance of 0 m, the probability of detecting the drone remained at 100% for depths $\leq \sim 1.0$ m (Figure 4.4A). For horizontal locations > 0 m, the probability of detecting the drone tag dropped to 0% at water depths ≥ 0.8 m. For water depths ≥ 0.5 m, the probability of detecting the drone tag dropped below 100% at tag heights ≤ 0.2 m (Figure 4.4B). Electrical current and percentage of RF ranged from 0.5 A and 84% (at 1.1 m deep) to 3.3 A and 14% (at 0.2 m deep) during drone tag testing.

The *in situ* probability of detecting a tagged fish on Antenna 2 for *Fundulus heteroclitus* known to have passed through this antenna was 0.933 (642 'successes' out of 688 trials). Water depth had a significant negative effect on *in situ* detection probability ($z = -2.897$; $p = 0.004$; Figure 4.5). The predicted detection probability of tagged fish declined from near 1.0 at water depths near 0 m to 0.8 at a water depth of 1.0 m (Figure 4.5). These data were collected throughout the vertical array period; during these detections, mean water

depth was 0.35 ± 0.21 m (S.D.), electrical current averaged 2.26 ± 1.15 A (S.D.), and mean RF noise was $21.8 \pm 21.8\%$ (S.D.).

Movement patterns Based on the criteria used to determine a valid move, the vertical array detected 1,112 movements; 624 were ingress and 488 were egress. The vertical antenna array detected subsequent moves in opposite directions in 72.5% of the cases. Thus, 27.5% of moves in one direction were not followed by moves in the opposite direction. *Fundulus heteroclitus* generally moved upstream through the array with flooding tides and downstream with ebbing tides; 84.5% of movements occurred in the direction of tidal flow (Figure 4.6). Mean water depth when fish moved through the array (\pm S.D.) was 0.29 m (\pm 0.21 m) upon ingress above the array and 0.43 m (\pm 0.18 m) upon egress below the array. The probability of movement upstream was negatively related to hourly water depth during ebb tide; at the end of ebb tide (low water depths) some fish would begin their movement upstream (Figure 4.6). During flood tides, the probability of ingress remained high across all hourly water depths. Hourly depth, tidal current, and the interaction between the two were contained in the most parsimonious model (Nagelkerke $r^2 = 0.702$; Table 4.3); this model received the majority of support.

Cormack Jolly Seber parameter estimates: apparent survival and detection probability

Forty-two of the original 44 tagged individuals were resighted between 9 November 2010 (Occasion 2) and 15 August 2011 (Occasion 167) (Figure 4.7). Mean daily water temperature over this time period ranged from 0.8°C on 8 December 2010 (Occasion 26) to 34.6°C on 30 May 2011 (Occasion 153; Figure 4.7). The greatest CJS detection probability occurred during a three week period after marking (Occasions 2 - 23) and during February

2011 (~ Occasions 80 - 105); high detection probability during these periods corresponded with warmer water temperatures in autumn and winter. The coefficient for water temperature was positive (warmer water temperatures led to higher detection probability via greater fish activity) and the 95% credible intervals (CI) did not contain zero during the vertical antenna period (Occasions 1-111) (Table 4.4). The water temperature effect during the horizontal antenna period (Occasions 112-167) was negative (warmer water resulted in lower detection probability via reduced fish activity). Convergence of chains of initial values to stable posterior distributions occurred within the burn-in period for logistic model parameters used to estimate detection probability by occasion. Median occasion-specific estimates of detection probability fluctuated over the study; the width of the credible interval about detection probability for each occasion averaged 64% of the median detection probability for each occasion (Figure 4.7).

Convergence to a stable posterior distribution of apparent survival occurred rapidly (after roughly 1,000 iterations). The median estimate of daily apparent survival (2.5% and 97.5% CI) was greater during period one (0.992 (0.988 - 0.996); warmer period) than during period two (0.979 (0.970 - 0.986); period with a series of cold temperatures); the CIs did not overlap between the two periods. *Fundulus heteroclitus* had higher apparent survival during period one than period two (Figure 4.8). There was low overall apparent survival of tagged *Fundulus heteroclitus* over the nine month monitoring period (~5% remaining after 280 days).

DISCUSSION

This study builds on the growing body of research using PIT tags to study saltwater fish *in-situ* (McCormick and Smith 2004; Adams et al. 2006; Meynecke et al. 2008; Hering

et al. 2010; Adams et al 2011; Barbour et al. 2012). Autonomous detection equipment recorded a large number of resightings on a nearly continual basis throughout the nine month monitoring period. The high temporal resolution of resightings allowed precise estimates of CJS model parameters and temporally fine-scale (hourly) movement patterns of an important salt marsh fish species.

Field estimates of apparent survival and detection probability using CJS model Our estimate of *Fundulus heteroclitus* apparent survival applies to the entire Porters Creek marsh both upstream and downstream of the antenna array. We were restricted to estimating apparent survival rather than true survival because we worked in an open system where marked fish may have permanently emigrated. However, estimates of apparent survival may be close to true survival for this species, given its small home range area (~ 100 m²) (Lotrich 1975; Meredith and Lotrich 1979; Teo and Able 2003) and high site fidelity to home creeks (Sweeney et al. 1998; Teo and Able 2003; Skinner et al. 2005). Fidelity to a single study system appears to be the case for Porters Creek; out of 300 PIT tagged fish released in this creek in 2013 (see Chapter 5) only 18 were recaptured in 180 traps set (3810 total *Fundulus heteroclitus* captured) outside of Porters Creek (up to 300 m either side of the mouth of the creek). Of these 18 tagged fish, 15 were subsequently resighted by the antenna array in Porters Creek (83% resighting rate). Thus, although some tagged fish were shown to move out of Porters Creek, trapping recaptures suggest that they stay within or in close proximity to the creek mouth and antenna resightings indicate that the vast majority of fish return to the creek after using nearby habitats.

Our results confirm prior work that *Fundulus heteroclitus* is a short-lived species. Using fish scales, Kneib and Stiven (1978) estimated ages of *Fundulus heteroclitus* (of similar sizes to this study) that were collected from a nearby North Carolina marsh; those authors reported that in August ~ 60% of their sample was age-0 fish with few fish making it past their second or third year of life (> age 1 or 2). Similarly, we found low survival of *Fundulus heteroclitus* ≥ 50 mm TL (likely older age-0 and younger age-1 fish when they were tagged). We found that CJS detection probability and apparent survival varied over a nine month period; past research using traditional gears does not have this temporal resolution. However, our overall estimate of apparent survival is similar to that of Meredith and Lotrich (1979). The total annual mortality rate (Z) of 4.49, calculated from our estimate of apparent survival, is close to the Z of 4.74 estimated from the declines in Meredith and Lotrich's (1979) abundance estimates of *Fundulus heteroclitus* in a Delaware salt marsh.

During period 2, the water temperature dropped to near freezing on multiple occasions. Over many of the occasions during this period the water temperatures were below the thermal optimum for *Fundulus heteroclitus* growth (Garside and Morrison 1977). While low water temperatures (< 5°C) over multiple days in the colder period may not have directly caused mortality of *Fundulus heteroclitus* (Fangue et al. 2006 saw high survival even at freezing temperatures), reduced activity levels may have made them more vulnerable to predation by species such as colonial (Ardeidid) wading birds and double-crested cormorants *Phalacrocorax auritus*.

Some CJS model assumptions may have been violated using PIT tags and autonomous arrays to collect resight data. The readers collected data continuously and this

type of sampling violates the assumption of instantaneous resighting. However, Hargrove and Borland (1994) reported that estimates from CJS models are not badly affected by violations of this assumption. Another assumption that was violated is that emigration from the study area is permanent. Temporary emigration of tagged *Fundulus heteroclitus* may have occurred during our study and can negatively bias estimates of CJS detection probability; however, estimates of apparent survival remain unbiased if temporary emigration is random so that all marked individuals have the same probability of being resighted (Williams et al. 2002). A frequency plot of the total number of occasions over which each individual was resighted showed no signs of extreme heterogeneity in CJS detection probability (e.g. bimodality). However, data were right-skewed, suggesting some heterogeneity in detection probability (Abadi et al. 2013). Heterogeneity in CJS detection probabilities among tagged individual has a negligible effect on survival rate estimates (Carothers 1979; Royle 2008; Abadi et al. 2013).

In contrast to these violations, other assumptions of the CJS model were reasonably satisfied. Tagged *Fundulus heteroclitus* were randomly selected from traps in order to obtain a representative subsample from the population inhabiting Porters Creek. *Fundulus heteroclitus* is not an open-water schooling species, so behavior, movement and survival of tagged individuals were considered independent among tagged fish.

Water temperature influenced the CJS detection probability. *Fundulus heteroclitus* maintains normal activity at water temperatures between ~ 12 and 30°C (Garside and Morrison 1977; Sidell et al. 1983). This range of thermal preference is consistent with the positive relationship between CJS detection probability and winter water temperatures which

often fell below 12°C. During the horizontal antenna period, detection of *Fundulus heteroclitus* decreased when the water temperature was occasionally above 30°C.

Although water depth influenced *in situ* probability of detecting a tag, it did not influence CJS detection probability for either array. This result makes sense considering the differences in how the effects of water depth are modeled with these two approaches. The *in situ* model estimates the probability of detecting the pass of a drone or fish at a specific water depth. For the CJS model, mean depth over an entire occasion was used to estimate detection probability. Although mean water depth varied among occasions, there was always a period within each occasion when water depths were low and tagged fish could be detected.

Vertical antenna performance and Fundulus heteroclitus behavior The hydroperiod (frequency and duration of flooding) of tidal creeks along the U.S. South Atlantic coast affects patterns of marsh use by resident and transient nekton (Rozas 1995; Kneib 1997; Allen et al. 2007). Tidal frequency and flooding duration control accessibility to the salt marsh by fishes and crustaceans while tidal amplitude influences the area of habitat available (Kneib 2003). The vertical antennas did not detect 100% of the tagged fish passing them; 27.5% of movements in one direction were followed by another movement in the same direction rather than being followed by movement in the opposite direction. However, the vertical antennas did document ingress and egress from which we could glean information on tidally-mediated use of creek habitats by adult *Fundulus heteroclitus*.

Attenuation of electrical current during deeper water periods reduced the detection of PIT tags. Therefore, any discussion of *Fundulus heteroclitus* behavior has to consider antenna performance (electrical current) that declined as water depth increased. Attenuation

of electrical current led to a zero *in situ* detection probability of the drone tag at water depths >1.0 m when passage was immediately adjacent to the vertical sides of the antenna (0 m horizontal locations). For other horizontal locations, the probability of detecting the drone tag dropped at 0.5 or 0.8 m water depths (depending on the height of the drone tag). This result suggests that not all movements of PIT tagged fish were detected by the array during periods of deeper water in the study creek.

Despite the fact that it generally did not perform as well as other antennas (lower electrical current), the *in situ* detection probability of tagged fish on Antenna 2 was high across a range of water depths and remained above 70% at water depths between 0.8 and 1.0 m. Thus, the *in situ* detection probability of tagged *Fundulus heteroclitus* is mostly consistent with predictions from drone tag data and we infer that *Fundulus heteroclitus* mostly passed near the vertical sides of the antenna (horizontal location = 0 m) when water depths were less than 0.8 m. Given that water depths were greater than 0.8 m roughly 26% of the time over the period when the vertical array was used, our antenna configuration did not capture all *Fundulus heteroclitus* movements. This finding is a likely reason for reduced number of defined emigrations (occurred during deeper water periods) relative to immigrations. The detection efficiency of the middle antenna in the vertical array (0.933) is comparable to the Hering et al. (2010) study (mean = 0.92) and greater than the Adams et al. (2006) study (0.67); Hering et al. (2010) measured proportional detection of one antenna based on the number of tagged fish detected by two antennas in their array while Adams et al. (2006) measured the proportion of tagged fish detected that were physically moved with a net past one antenna.

Increased detections of FDX PIT tags occurred when more of an antenna was out of saltwater. For studies conducted in waters of similar salinities, our recommendation for vertical antennas of similar materials and placement (with the long axis of the antenna horizontal) is to work in waters less than ~ 0.6 m deep if detection near 100% is needed. However, even with missed detections, the frequency of resightings is much higher with this gear than with traditional approaches, resulting in robust estimates of CJS model parameters (Hewitt et al. 2010). Not being able to assign a fate to every marked fish (survived, died, or emigrated) does have ramifications for some analytical approaches where all marked animals have to be assigned a fate, such as Kaplan-Meier survival analysis (Pollock et al. 1990; Williams et al. 2002).

There are several ways to potentially increase *in situ* detection probability to develop increasingly more accurate estimates of movement patterns and demographic parameters of saltwater fishes such as *Fundulus heteroclitus*. Hering et al. (2010) maintained high detection efficiency of PIT tagged juvenile salmon in relatively deep salt water by having the long axis of a vertical antenna running vertically (i.e., more of the antenna is in the air across all water depths compared to when the long axis is horizontal). We chose not to use this deployment because we were concerned that it would alter the behavior of *Fundulus heteroclitus* (and other salt marsh organisms) given the narrow restriction relative to the natural width of the creek channel where the array was located. Where permitted and feasible based on shoreline stability and impacts to salt marsh, orienting antennas with the long axes vertical may help to maximize the perimeter of an antenna that remains exposed to air when used in saltwater and help maintain the electrical current above a threshold where

detections fail, over a wide range of water depths. Given imperfect *in situ* detection probability by a single antenna, redundancy in the number of antennas comprising a detection array is one method for increasing the probability of detecting PIT tagged fish. A valid move in our study required detection by at least two antennas in appropriate order (i.e. for up- or downstream movement) within a ten minute period. As an example of the benefit of a multiple-antenna array, the predicted detection probability of the drone by a single antenna at a depth of 0.6 m, tag height of 0 m, and horizontal location other than 0 m, would be 0.77. This scenario would yield a combined probability of detecting a valid move of 0.59 with a two-antenna array but 0.86 with a three-antenna array.

Fundulus heteroclitus appears to maximize periods over which the vegetated marsh surface can be accessed following low tide (Weisberg and Lotrich 1982; Teo and Able 2003; Bretsch and Allen 2006; Allen et al. 2007). It entered the study creek (moved above the array) shortly after the tide started flooding. This species uses the direction of tidal flow to likely reduce energetic expenditures by generally moving in the direction of the tidal current (Sweeney et al. 1998). Our data confirm these observations. *Fundulus heteroclitus* ingressed above the array when the water was relatively shallow; this movement occurred during the very late stages of ebb tide or early in the flood tide. Previous research (Gibson 1988; Kneib and Wagner, 1994) has suggested that the risk of stranding on ebb tide may cause salt marsh fishes to egress at water depths greater than those upon ingress. Our results confirm this as *Fundulus heteroclitus* emigrated from Porters Creek as early as the beginning of ebb tide. The timing of this tidally mediated movement likely helps to maximize growth rates of *Fundulus heteroclitus* because it extends the time period over which they can feed on the

marsh surface (Kneib 1993; Haas et al. 2009). Butner and Brattstrom (1960) observed that *Fundulus heteroclitus* collected over flood tides in tidal creeks had empty guts while those collected over ebb tides had full guts, suggesting that fish are feeding on the flooded marsh surface.

FDX PIT tags in 12.5 mm sizes have now proven to be effective for studying movements and demographics of small-bodied saltwater fishes (Hering et al., 2010; this study) and future comparisons with recently available 12 mm HDX PIT tags are warranted. Further refinements to construction of PIT tags and custom detection gears are likely to increase the use of this technique in marine and estuarine habitats. Future work (Chapter 5) will estimate survival across multiple systems to gain a better understanding of habitat-specific productivity in this species.

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Table 4.1. Chronology of events related to PIT tagging and resighting *Fundulus heteroclitus* with two custom-made autonomous detection antenna arrays near the mouth of Porters Creek, North Carolina between 8 November 2010 and 4 October 2011.

Event date(s)	Event(s)	Sampling occasion(s)
8 - 24 Nov 2010	Tagging (8 Nov 2010) and data collection with three vertical antennas	1 – 17
25 – 29 Nov 2010	Multiplexer malfunction (no data)	
30 Nov 2010 – 3 Mar 2011	Data collection	18 - 111
4 Mar – 13 Apr 2011	Antenna maintenance (no data)	
14 Apr – 10 May 2011	Commencement of data collection with single horizontal antenna	112 - 138
11 May 2011	Power failure (no data)	
12 May 2011	Data collection	139
13 – 16 May 2011	Antenna maintenance (no data)	
17 May - 5 Jun 2011	Data collection	140 - 159
6 – 23 Jun 2011	Detections not date-stamped	
24 Jun 2011	Download data (occasion 160 = 6 -24 June)	160
25 – 27 Jun 2011	Detections not date-stamped	
28 Jun 2011	Download data (occasion 161 = 25 – 28 June)	161
29 Jun – 1 Jul 2011	Detections not date-stamped	
2 Jul 2011	Download data (occasion 162 = 29 June - 2 July)	162
3-13 Jul 2011	Detections not date-stamped	
14 Jul 2011	Download data (occasion 163 = 3 – 14 July)	163
15 – 20 Jul 2011	Detections not date-stamped	

21 Jul 2011	Download data (occasion 164 = 15 – 21 July)	164
22 – 31 Jul 2011	Detections not date-stamped	
1 Aug 2011	Download data (occasion 165 = 22 July – 1 Aug)	165
2 – 7 Aug 2011	Detections not date-stamped	
8 Aug 2011	Download data (occasion 166 = 2 – 8 Aug)	166
9 – 14 Aug 2011	Detections not date-stamped	
15 Aug 2011	Download data (occasion 167 = 9 – 15 Aug)	167
16 – 19 Aug 2011	Detections not date-stamped	
20 Aug 2011	Download data (occasion 168 = 16 – 20 Aug)	168
21 – 31 Aug 2011	Detections not date-stamped	
1 Sep 2011	Download data (occasion 169 = 21 Aug 21 – 1 Sep)	169
2 – 21 Sep 2011	Data collection	170 - 189
22 Sep 2011	Power failure (no data)	
23 Sep – 4 Oct 2011	Data collection through last detection (4 Oct 2011)	190-201

Table 4.2. Logistic regression models relating drone PIT tag detections by a custom-made vertical antenna to water depth (depth), tag height off the creek bottom (tag height), and horizontal location within the perimeter of the antenna (location). The null model includes the intercept term only. QAICc = quasi Akaike Information Criteria; a lower QAICc score indicates greater model parsimony with the data than a higher score. Models are ranked from lowest to highest QAICc scores. Δ QAICc is the difference between the QAICc value for the best fitting model and each model that was fitted. Number of model parameters (including penalty for over-dispersion) = k . The Akaike weight (w_i) represents the proportional support for each model.

Model	k	QAICc	Δ QAICc	w_i
depth + tag height + location + depth*tag height	8	80.3	0	0.57
depth + tag height + location + depth*tag height + depth*location + tag height*location	14	81.9	1.6	0.26
depth + tag height + location + depth*tag height + depth*location	11	83.7	3.4	0.10
depth + location	6	86.0	5.73	0.03
depth + tag height + depth*tag height	5	87.8	7.46	0.01
depth + tag height + location	7	88.1	7.79	0.01
depth	3	92.1	11.8	0.00
depth + tag height	4	94.1	13.8	0.00
null	2	211.1	130.8	0.00
tag height	3	212.1	131.8	0.00
tag height + location	6	215.4	135.1	0.00

Table 4.3. Logistic regression models relating movement of PIT-tagged *Fundulus heteroclitus* (1 = ingress, 0 = egress) through an autonomous array of vertical antennas in Porters Creek, North Carolina. Movement was modeled as a function of hourly water depth and tidal current (tide: ebb or flood). The null model includes the intercept term only. QAICc = quasi Akaike Information Criteria; a lower QAICc score indicates greater model parsimony with the data than a higher score. Models are ranked from lowest to highest QAICc scores. Δ QAICc is the difference between the QAICc value for the best fitting model and each model that was fitted. Number of model parameters (including penalty for over-dispersion) = k . The Akaike weight (w_i) represents the proportional support for each model.

Model	k	QAICc	Δ QAICc	w_i
hourly depth + tide + hourly depth*tide	5	679.3	0	0.99
hourly depth + tide	4	689.6	10.3	0.01
tide	3	842.4	163.1	0.00
hourly depth	3	1345.0	665.7	0.00
null	2	1464.7	785.4	0.00

Table 4.4. Results of estimating covariates of detection probability when fitting the Cormack Jolly Seber model to detections of PIT tagged *Fundulus heteroclitus* by two antenna arrays in Porters Creek, North Carolina. The table lists the median, 2.5% credible interval, and 97.5% credible interval (CI) of each regression coefficient when modeling detection probability as a logistic function of water temperature when an array of three vertical antennas was used (Occasions 2 - 111) and when a horizontal antenna was used (Occasions 112 - 167).

Occasions	Parameter (description)	2.5% CI	median	97.5% CI
2 - 111	β_0 (intercept,logistic model; vertical antennas)	-0.803	-0.709	-0.566
	β_1 (temperature coefficient, vertical antennas)	0.208	0.233	0.255
112 - 167	β_0 (intercept,logistic model; horizontal antenna)	-0.112	0.056	0.273
	β_1 (temperature coefficient, horizontal antennas)	-0.192	-0.123	-0.066

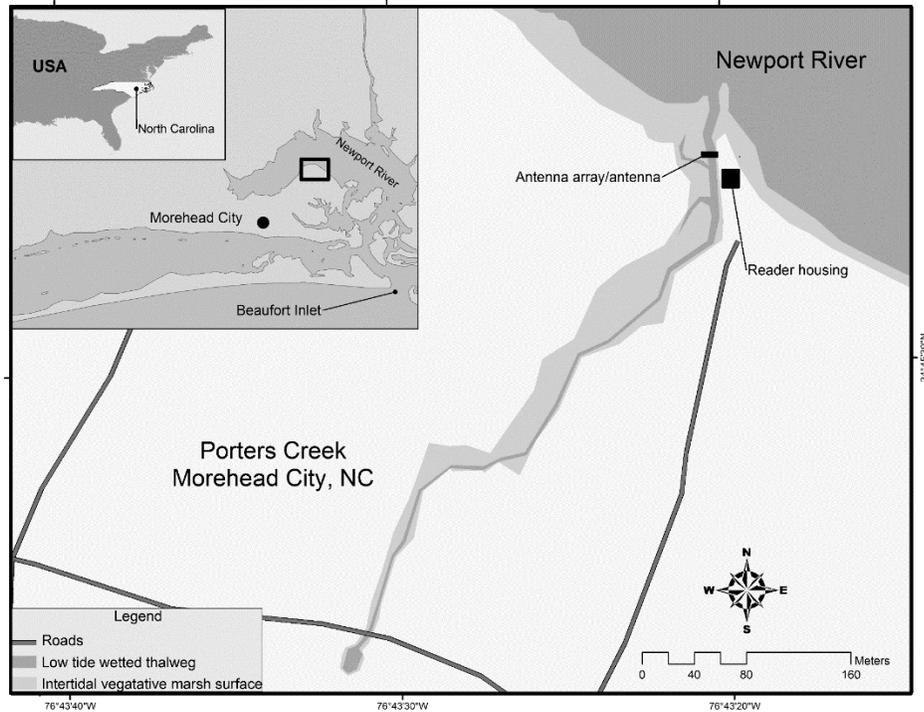


Figure 4.1. Map of Porters Creek, North Carolina, showing the location of custom-made autonomous antennas (three vertical or one horizontal) used to detect PIT-tagged *Fundulus heteroclitus* between 8 November 2010 and 4 October 2011. Map shows the areas of Porters Creek wetted at both high tide (light gray shading) and low tide (dark gray shading). Fish were captured and released in the area of the creek within 50 m of the array.

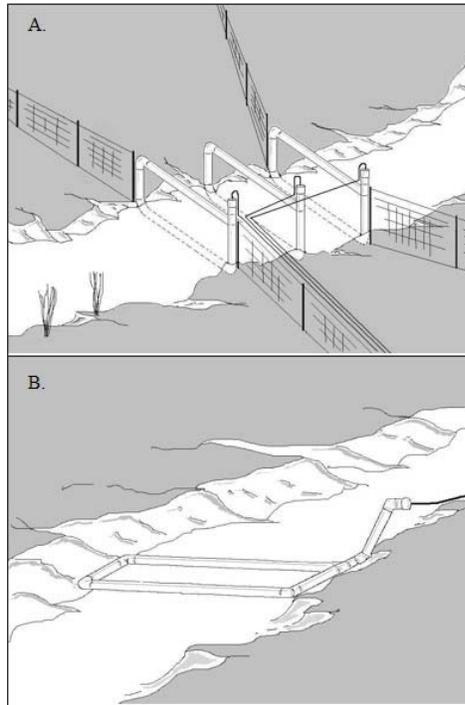


Figure 4.2. Diagrams of two different styles of antenna arrays placed in the channel of Porters Creek, North Carolina to detect PIT tagged *Fundulus heteroclitus* by: A) an array of three vertical antennas used between November 2010 and March 2011, and B) a single horizontal antenna used between March and October 2011.

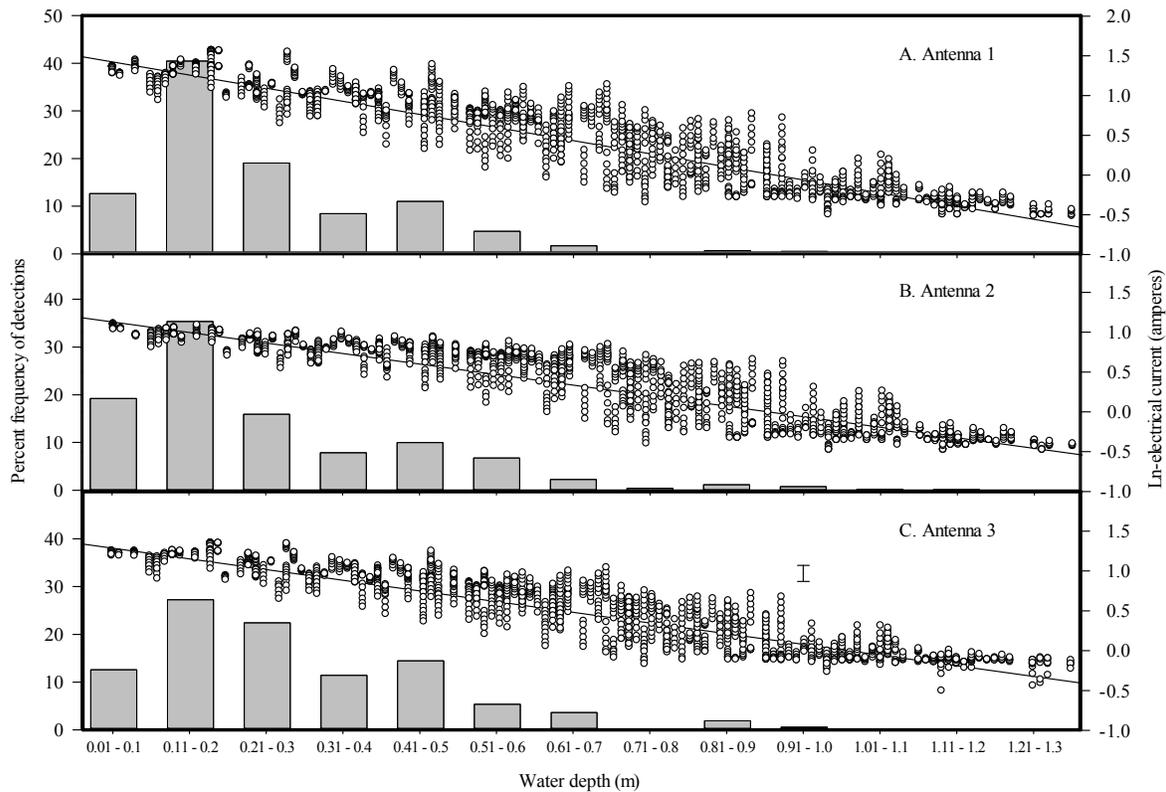


Figure 4.3. Plots of the percent frequency of detections (left y axis; vertical bars) and the natural logarithm values of autonomous electrical current (amperes) (right y axis; circles) vs. water depth when fish passed (m) (x axis) for each of three vertical antennas used to detect PIT-tagged *Fundulus heteroclitus* in Porters Creek, North Carolina between 9 November and 3 March 2011. Each pair of values for electrical current vs. water depth is represented by a circle while percent frequency of detections (by water depth bins) is represented by shaded bars. The x axis is scaled for both the binned and the discrete depth data. The predicted straight line in each panel represents results from fitting a least squares linear regression model (with significant slope) relating the natural logarithm values of electrical current to water depth at those time points when electrical current was supplied by the receiver.

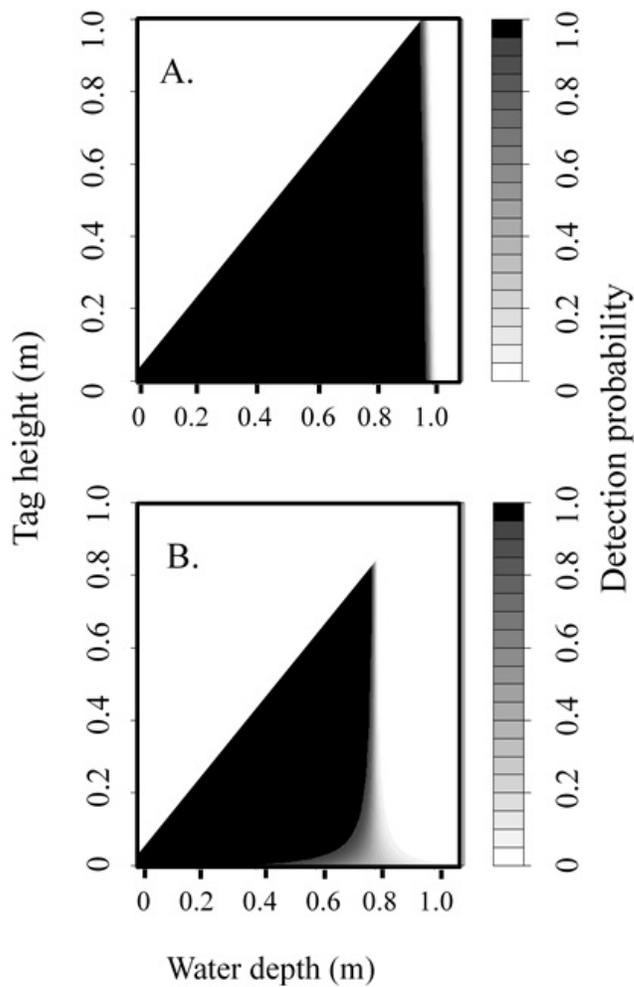


Figure 4.4. Predicted probability of detection (gray scale grid) of a 12.5 mm drone PIT tag passed through a custom-made antenna as a function of water depth (x axis) and tag height above the bottom of the creek (y axis). Predicted detection probabilities were separately modeled for a horizontal location (left to right within the perimeter of antenna) of 0 m (Panel A) and at all other horizontal locations (0.25, 0.5, and 0.75 m) (Panel B).

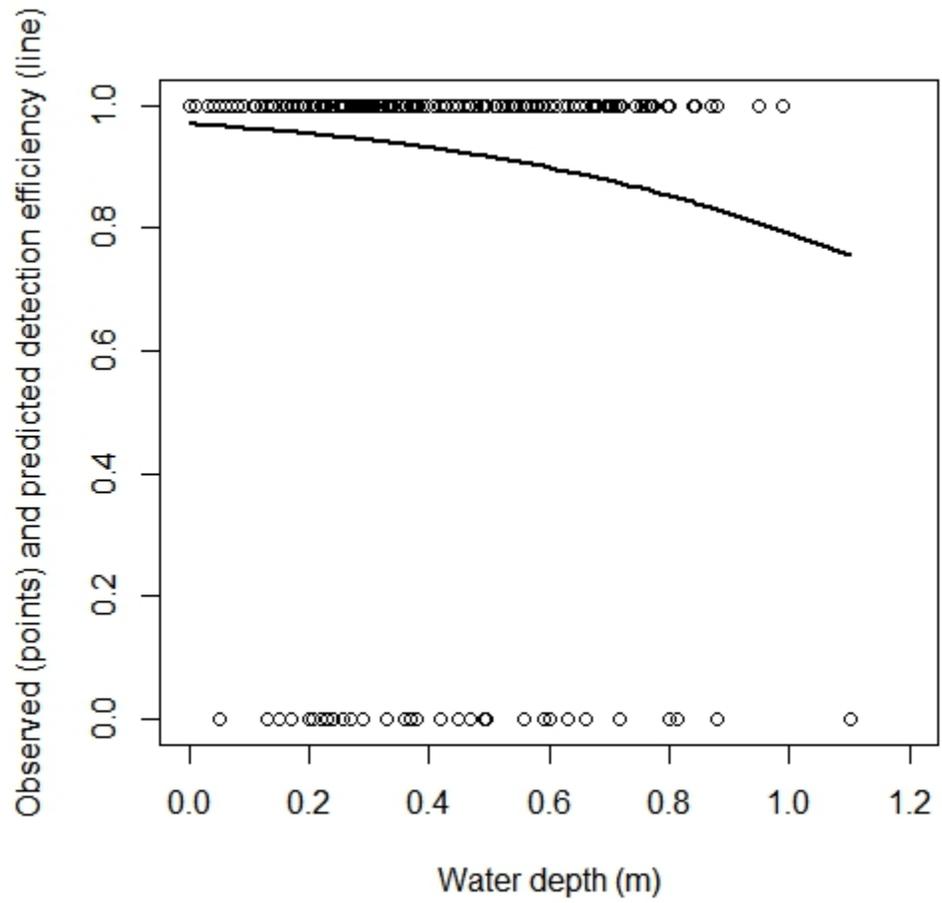


Figure 4.5. Predicted *in situ* detection probability (logistic model fit; line) of PIT tagged *Fundulus heteroclitus* (y axis) moving past an array of three vertical antennas in Porters Creek, North Carolina as a function of water depths (x axis). *In situ* detection probability here is the binomial success of the middle antenna of the array to detect a PIT tag. The observed data (open circles) represent moves where a fish was detected by all three antennas (y value = 1) or by only the outer two antennas and not the middle antenna (y value = 0).

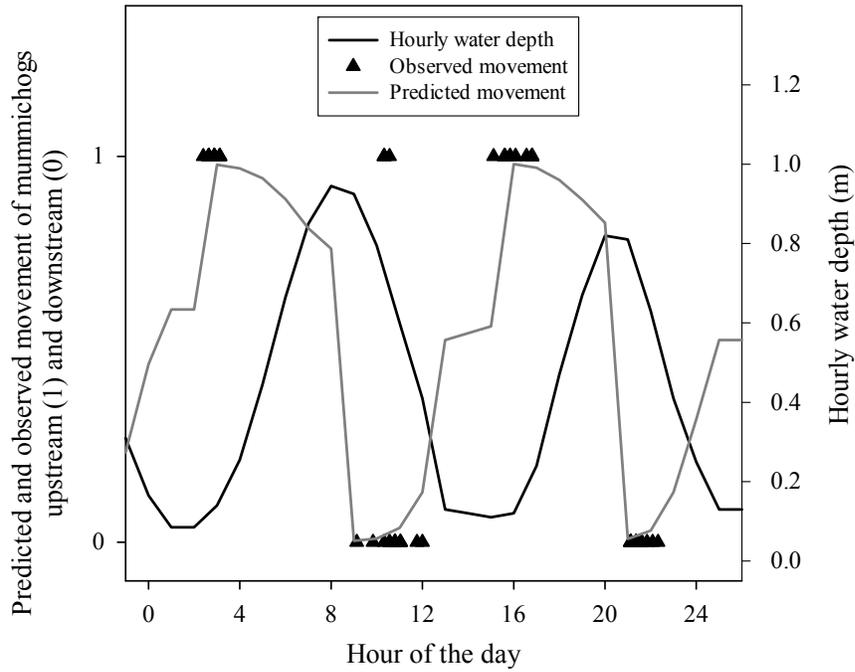


Figure 4.6. Observed ingress (1) and egress (0) (black triangles) and predicted ingress/egress (gray line) (left y axis) of PIT tagged *Fundulus heteroclitus* plotted over a diel cycle as a function of hourly water depth (solid black line; right y axis). Data were collected by an array of three vertical antennas on 19 November 2010 near the mouth of Porters Creek, North Carolina. See *Results* section for a description of the predictive fish movement model.

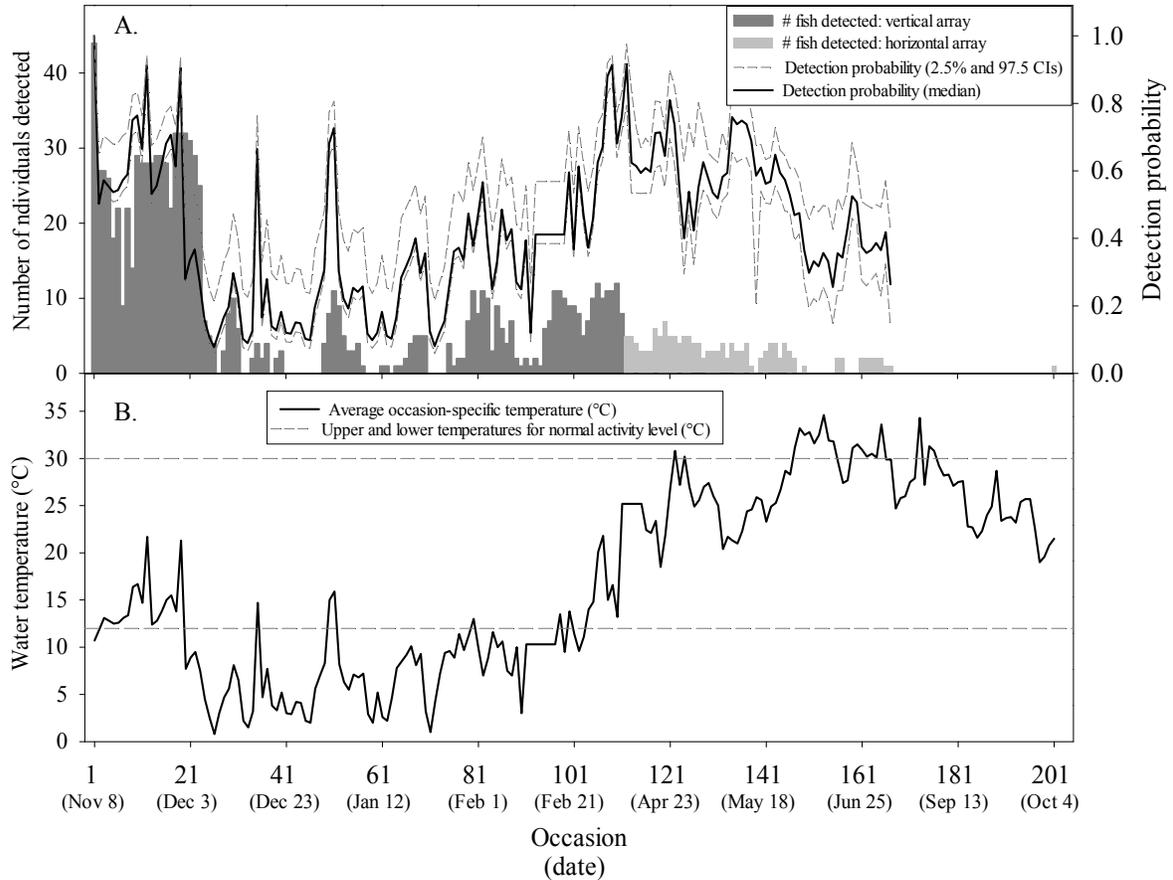


Figure 4.7. Panel A: Number of individual PIT-tagged *Fundulus heteroclitus* detected (left y axis) by an array of three vertical antennas (dark gray bars) (Occasions 1-111) and by a single horizontal antenna (light gray bars) (Occasions 112-201) in Porters Creek, North Carolina between 8 November 2010 (day of tagging) and 4 October 2011 (last occasion on which a tagged fish was detected). Detection probability for this figure was estimated by fitting a Cormack Jolly Seber model to antenna detection data for occasions (x axis) between 9 November 2010 (Occasion 2) and 15 August 2011 (Occasion 167). The occasion corresponding to each date on the x axis is in parenthesis. Median occasion-specific detection probability (right y axis) is graphed as the solid black line and 2.5 and 97.5% credible intervals about median detection probability as dashed gray lines. Panel B: Mean occasion-specific water temperature (°C) (y axis; solid line) and lower and upper water temperatures for normal activity levels of *Fundulus heteroclitus* (12 and 30°C, respectively; horizontal dashed gray lines) vs. occasion (x axis). Water temperatures over which normal activity of *Fundulus heteroclitus* is expected were estimated from Garside and Morrison (1977) and Sidell et al. (1983).

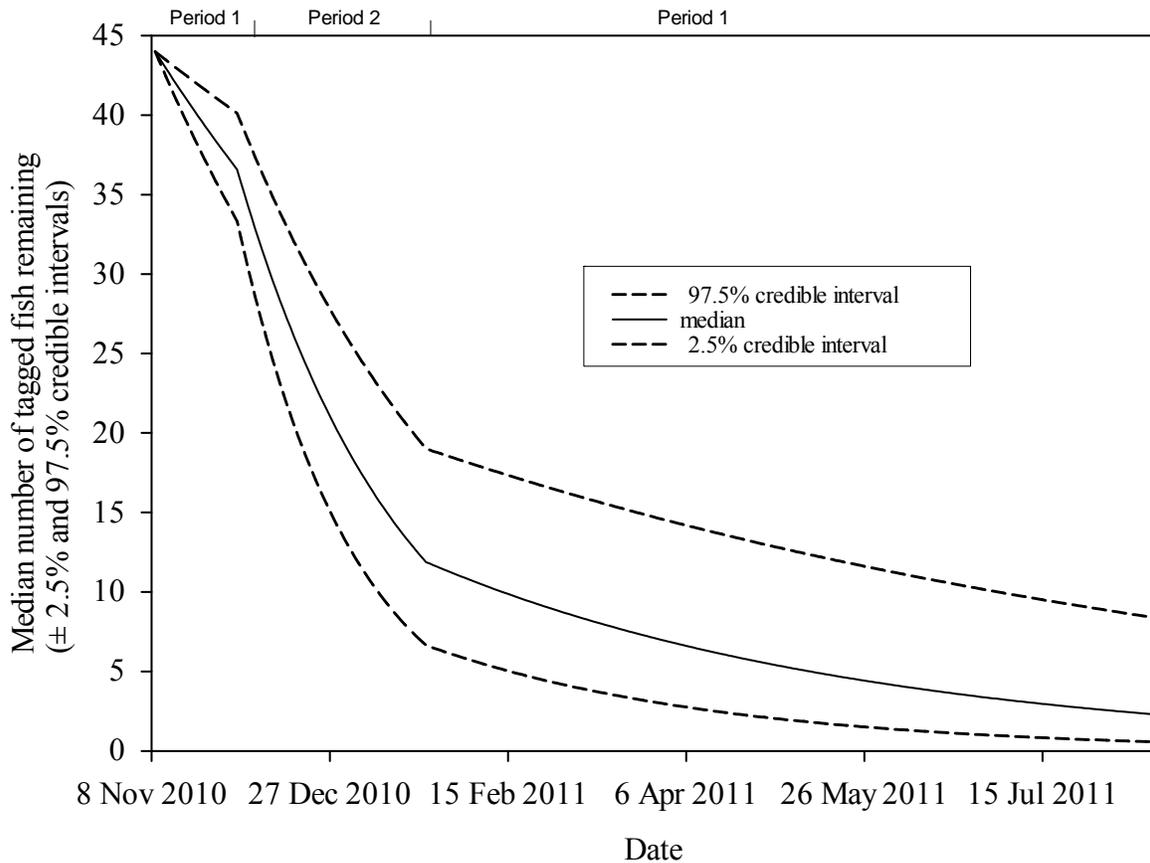


Figure 4.8. Estimated number of PIT tagged *Fundulus heteroclitus* surviving in Porters Creek, North Carolina based on the initial number of tagged fish ($n = 44$) on 8 November and based on the estimated apparent survival rates from a fitting Cormack Jolly Seber model to PIT tag resight data during Period 1 (8 November 2010 – 1 December 2010 and 24 January - 15 August 2011) and Period 2 (2 December 2010 and 23 January 2011). See *Results* section for estimates of apparent survival by period.

CHAPTER 5. SURVIVAL AND ABUNDANCE OF A TIDAL CREEK FISH ACROSS A DEVELOPING LANDSCAPE

Paul J. Rudershausen, Jeffrey A. Buckel, Joseph E. Hightower, Todd Dubreuil, Matthew J. O'Donnell, and Benjamin Letcher

ABSTRACT

Apparent survival and abundance of *Fundulus heteroclitus*, a dominant salt marsh fish, were estimated in North Carolina tidal creeks using models fitted to mark-resight and mark-recapture data. We then related these population metrics to natural habitat and anthropogenic disturbance factors measured at both the creek and watershed levels. Creek populations experienced high rates of loss (mortality plus emigration) which were similar and consistent among creeks and years. Sampling for tagged fish within and outside of study creeks showed high site fidelity for fish within each creek or near its mouth, suggesting that high loss rates largely result from mortality. We found a positive relationship between minnow trap catch-per-unit-effort (relative abundance) and absolute density in four creeks and used relative abundance as a proxy for absolute density in a total of six study creeks. Highest relative abundance values occurred early in each growing season and were associated with creeks with higher percentages of salt marsh; this suggests that reproduction rather than survival is sensitive to human impact. Results show that this species has low and consistent rates of survival among salt marsh creeks and watersheds of varying habitat qualities and that marsh coverage reflective of undisturbed systems is needed for this species to remain at high abundance levels. Natural resource planners should place a priority on preserving salt marsh in order to maintain abundance levels of this species, which is a critical source of trophic relay from tidal creeks to open-water estuaries.

INTRODUCTION

Salt marshes are intertidal habitats found along the coastlines of middle latitudes that provide ecosystem services such as contaminant filtration, carbon sequestration, buffering against storm surge, and habitat for fishes and crustaceans (Costanza et al. 1997; Portnoy et al. 1999). These ecologically important areas are sources of biological production that support recreationally and commercially important fish and shellfish stocks along the U.S. Atlantic coast (Turner 1977; Kneib 1997; Seabrook 2012).

There is a global trend of coastal development to imperil the ability of estuaries to serve as habitat for resident and transient fishes (Hinrichsen 1998). Salt marshes are threatened by human development in coastal North Carolina (Deaton et al. 2006) and elsewhere in the U.S. South Atlantic coastal plain (Dame et al. 2000). Specific threats to these habitats include eutrophication (Deegan et al. 2012), sea level rise (Donnelly and Bertness 2001; Craft et al. 2009), habitat loss (Kennish 2001) and habitat fragmentation (Kennish 2001; Mudd 2011). The relationships between demographics of important tidal creek species and habitat and urbanization effects remain largely unknown despite human threats to coastal areas. North Carolina fishery managers have recognized this data gap and identified the need for more fishery-independent data to determine the effects of wetland coverage on fish and invertebrate demographics in the state's estuaries (North Carolina Division of Marine Fisheries 2010). Additionally, on a broader geographic scope, the U.S. Environmental Protection Agency's Coastal Wetlands Initiative has a goal to better understand contributing stressors to coastal wetland loss (including salt marsh loss) (Environmental Protection Agency 2017). This study contributes towards filling these state and federal goals.

Previous researchers have described ideal indicator species through which to determine the extent of human impacts. Jones and Kaly (1986) believed that an ideal indicator is typically more abundant because it promotes the ease with which effects of anthropogenic disturbances can be detected. Hellowell (1986) believed that the bio-indicator should be a widely recognized and researched species. Multiple researchers believe that an ideal bio-indicator should readily accumulate pollutants yet be largely resilient to human impacts to allow for monitoring of effects of disturbances on non-lethal biological responses (Phillips 1980; Hellowell 1986; Wenner 1988). Ideal indicators are constantly exposed to conditions specific to environments from which they are sampled (Bilyard 1987; Jones and Kaly 1996; Raimondi and Reed 1996). Further, ideal indicators have been described as cornerstones of community and trophic structure (Underwood and Peterson 1988), have cosmopolitan distributions, and are readily quantified (Hellowell 1986).

Fundulus heteroclitus is the dominant resident fish species inhabiting salt marshes along the North American Atlantic coast (Kneib 1986; Kneib 1997; Able and Fahay 1998; Able et al. 2012). Based on published criteria for ideal bio-indicators, it is a good model for studying anthropogenic impacts on tidal creeks because of its abundance and role in salt marsh trophic dynamics (Kneib 1986; Kneib 1997), small home range, localized recruitment patterns, site fidelity to home marshes (Lotrich 1975; Sweeny et al. 1998; Skinner et al. 2005), and lethal and sub-lethal sensitivity to anthropogenic contaminants (Smith and Weis 1997; Van Veld and Nacci 2008).

Survival and abundance are important demographic variables used to assess estuarine fish stocks (Able 1999). Studies into the effects of disturbance on demographics of bio-indicators are relatively uncommon at the population level (Jones and Kaly 1996) and rare

for tidal creek nekton (Able 1999; Minello et al. 2003). Despite its widespread abundance, trophic importance, and usefulness as a species by which to gauge anthropogenic impacts on tidal creeks, the demographics of *Fundulus heteroclitus* have seldom been estimated along the Atlantic and Gulf coasts (except see Valiela et al. 1977; Meredith and Lotrich 1979; Teo and Able 2003) and, to the best of our knowledge, demographics have not been related to habitat and anthropogenic factors along the rapidly developing U.S. Atlantic coast.

Recognizing the potential for human impacts to its estuaries, the state of North Carolina has implemented a coastal habitat protection plan (Street et al. 2005). One of the goals of this plan is to identify strategic habitat areas: habitats of exceptional value for estuarine-dependent fish and shellfish species (Deaton et al. 2006) that are at risk of experiencing anthropogenic impact along the North Carolina coast (Jensen et al. 2014). Salt marsh is a ‘natural resource target’ identified as essential fish habitat in North Carolina while culverts, dredged (deepened) channels and developed land use (watershed imperviousness) are anthropogenic alterations implicated for negative effects on natural resource targets (Jensen et al. 2014). *Marxan*, a site-selection software developed for designing terrestrial reserves (Ball and Possingham 2000), is used to designate these habitats (including salt marshes) based on 1) specific ‘targeted’ habitat features and, 2) a ‘cost’ layer of anthropogenic alterations assumed to be equivalent to habitat degradation (Jensen et al. 2014). Costs in the North Carolina strategic habitat selection process include human activities, habitat features, and water quality indicators that can affect the condition of natural resource targets (Jensen et al. 2014). However, the influence of costs on components of fish production have not been investigated. Examining the assumption that anthropogenic impacts lead to reduced fish survival and abundance was a motivation for this research.

Among coastal habitats, tidal creeks are sentinels for monitoring anthropogenic impacts due to their direct connection to the surrounding landscape (Holland et al. 2004; Sanger et al. 2013). Here, passive integrated transponder (PIT) tags, autonomous antenna arrays, and traditional tag recapture data were used to estimate apparent survival and abundance of *Fundulus heteroclitus* in multiple tidal creeks and years. We then tested for a relationship between *Fundulus heteroclitus* population demographics and habitat and urbanization factors. This study builds on previous research of tidal creek nekton communities along the southeastern U.S. coast (Krebs et al. 2014; Rudershausen et al. 2016; Chapter 2) by relating demographics of an important species to habitat and anthropogenic factors along a gradient of impacts in a section of the rapidly developing North Carolina coastline.

METHODS

Study areas Sampling occurred in six first-order tidal creeks in Carteret County, North Carolina (Table 5.1). Stream order (Hettler 1989) and location (Minello et al. 2003) of tidal creeks in the landscape are determinants of the distribution and abundance of estuarine nekton (Minello et al. 2003; Sanger et al. 2013); the six tidal creeks where this research occurred are roughly equally positioned from their downstream waterbodies and distances to ocean inlets (Figure 5.1). This similar first-order classification and position in the landscape permits a more meaningful comparison among study creeks than if stream order varied (Sanger et al. 2013).

We installed detection antenna arrays (hereafter arrays) to collect resight data from *Fundulus heteroclitus* tagged with PIT tags in four first-order salt marsh creeks. These creeks were: Porters, a 600-m long creek with unrestricted (non-culvert) flow downstream to

the Newport River Estuary; Pelletier West, a 250-m long creek with a culvert connecting it to lower Pelletier West Creek; Atlantic Veneer, a 250-m long creek with culvert access to Taylor Creek; and Spooners, a 200-m long creek with culvert access to lower Spooners Creek. All four creeks were also sampled with minnow traps and cast nets for physical recaptures of tagged fish and estimating catch-per-unit-effort (CPUE). Two additional creeks were sampled for CPUE data only. These creeks were: Pelletier East, a 0.33 hectare pond that has a narrow fringing marsh (~ 2 m wide) and bounded by two culverts, one leading upstream to a creek reach above the study area and one downstream to lower Pelletier East Creek and Bogue Sound; and Webb, a manmade marsh-less canal with direct (non-culvert) access downstream to Lower Spooners Creek. The area in each creek over which we characterized habitat and where the majority of biological sampling occurred was either upstream of a parent waterbody (Porters and Webb Creeks), upstream of a culvert (Pelletier West, Spooners, and Pelletier East Creek), or between upstream and downstream culverts (Pelletier East Creek). Except for completely sub-tidal Webb Creek, each creek was considered intertidal with the vegetated marsh void of water over low tides. The channels in Porters, Atlantic Veneer, and Spooners Creeks have rivulets of water at low tide while the majority of the channel in Pelletier West Creek remains inundated. Each creek possesses a varying amount of fringing intertidal marsh dominated by saltmarsh cordgrass *Spartina alterniflora* (Loisel) except for Webb Creek which had no *Spartina alterniflora*. The duration that the vegetated marsh floods over each semi-diurnal tide is roughly the same among the five creeks with salt marsh. Each creek experiences tidal amplitudes of roughly 1.0 m during spring tides and 0.7 m during neap tides (P.J. Rudershausen, pers. obs.).

Field sampling- For the creeks with PIT tag arrays, fish to be PIT tagged were collected using 6.4 mm square mesh wire mesh minnow traps baited with dried pet food. Fish were tagged in either two or three batches (depending on year). Fish were first tagged in April of each year and subsequent batches were tagged later in the growing season (Table 5.2). We tagged fish in Porters and Pelletier West Creeks over four springs/summers (2011-14) and in Atlantic Veneer and Spooners Creeks over three springs/summers (2012-14).

The sizes of *Fundulus heteroclitus* PIT tagged in this study (≥ 41 mm total length (TL)) covers roughly the size range of adults of this species (Kneib and Stiven 1978). The minimum fish size that was PIT tagged was almost equal to the minimum size (39 mm) retained by 6.4 mm wire mesh minnow traps (pers. obs.). Two sizes of PIT tags were used to mark fish. Fish 41-59 mm TL were tagged with 8.4 mm (0.03 g) PIT tags and fish ≥ 60 mm TL were tagged with 12.5 mm (0.10 g) PIT tags. Only 12.5 mm PIT tags were used in 2011. A tank study (Brewer et al. 2016) found that *Fundulus heteroclitus* in each size group retained PIT tags and had survival and growth rates similar to untagged conspecifics over the range of fish sizes tagged with each tag size; details of the surgical procedure used in this study are found in Brewer et al. (2016). Each tagged individual was released in the vicinity of its capture location once normal swimming behavior resumed.

PIT tag receivers and custom-made arrays were used to passively collect mark-resight data to estimate apparent survival of tagged fish. Arrays were located at or near the mouth of each creek. The size and composition of antennas and receivers is described elsewhere (Rudershausen et al. 2014; Chapter 4). The configuration of the arrays differed among creeks (Figure 5.2) due to creek channel morphology and what was permitted by the North Carolina Division of Coastal Management for installation. Porters Creek had a single

antenna that was horizontal (flat) on the creek bottom and anchored to the sediment where the creek transitions from a rivulet of water at low tide to standing water that persists over all tides. For detection by a horizontal ‘swim over’ antenna, a PIT-tagged fish must swim within roughly 0.25 m of the antenna when it is submerged (Rudershausen et al. 2014). Porters Creek also had a vertical antenna in its array (Figure 5.2A). The vertical antenna is a ‘swim through’ antenna orientation (Rudershausen et al. 2014) that has higher detection probabilities than the ‘swim over’ design (Bass et al. 2012; unpublished data). The other three creeks were outfitted with vertical ‘swim through’ antennas in the center of their respective creek channels (Figures 5.2B-D).

Arrays in Porters, Pelletier West, and Spooners Creeks were connected to a 24-V FS-1001-M multiplexing receiver (multiplexer) (Destron Fearing, St. Paul, MN) capable of determining the unique code of each PIT tag. At Atlantic Veneer Creek, a Destron Fearing 24 V FS-1001A PIT tag receiver or a multiplexer was used. Unlike the multiplexer, the FS-1001A can only interface with one antenna at a time and does not provide the specific date and time of each detection; detections at Atlantic Veneer Creek were assigned the same date of the ~weekly manual downloads of the data (Table 5.2).

Minnow trap sampling (independent of trapping to tag fish) was used to estimate CPUE in the six study creeks and, for the four creeks where fish were PIT tagged, to obtain numbers of tagged and untagged individuals. Each creek was sampled with 6.4 mm wire mesh minnow traps baited with dried pet food and fished on a roughly monthly basis from spring through fall of each year of the study. Each creek was divided into ten strata of equal length and one trap was fished per stratum on 3-hour soak times around high tide in each creek except for Porters Creek where typically two traps per strata were deployed because of

its larger size than the other creeks. Additionally, 1-2 traps were placed downstream to recapture tagged fish that temporarily moved outside of the creek or below a culvert. We soaked traps for 3 hours in the creeks to give fish the opportunity to find and enter traps, including individuals far removed from a trap placement or in creeks with low densities. Traps were set around high tide to capture fish at densities reflective of their dispersal over full high-tide wetted areas (both vegetated and non-vegetated habitats) (Kneib 1997; Allen et al. 2007).

We also used an actively deployed cast net (1.2 m diameter, 6 mm square mesh) in each creek with an antenna array to estimate the ratio of tagged to untagged individuals. The ratio from cast net samples was compared to the ratio from passively deployed minnow traps to test for potential trap happiness or shyness by the passive gear type (Nichols et al. 1984). Cast netting was done monthly around low tide in each creek at a single location that logistically allowed cast net deployment and had high densities of fish. We assumed that the ratio of tagged:untagged fish in a sample did not change as a function of the tidal cycle.

Upon retrieval of each trap and cast net, fish were scanned for PIT tags using a 2001 F-ISO handheld receiver (Biomark Inc., Boise, ID) and the total number of *Fundulus heteroclitus* was counted. PIT tagged fish along with a subsample of untagged fish from each trap (up to 30 if the catch allowed) were measured for TL (mm). The number of unmeasured fish in each size category (<41 mm TL vs. \geq 41 mm TL) was estimated using the ratio of these two size groups from the measured subsample in each trap. This resulted in numbers of tagged and untagged fish in the \geq 41 mm size category. Both tagged and untagged fish were released back into their respective creeks after capture.

Examination of study area boundaries and site fidelity Apparent survival (Φ) confounds losses due to mortality and permanent emigration from a study area (Kéry and Schaub 2012; Schaub and Royle 2013). The extent to which Φ underestimates true survival (S) depends on the configuration of the study area as well as the dispersal behavior of the study species (Schaub and Royle 2013). In estimating rates of Φ we considered the study area of each creek to be both above the array as well as below it to the parent waterbody. If site fidelity is high, rates of Φ will approach or equal rates of S (Sandercock 2003).

Three auxiliary sampling approaches were used to determine the effective study area of each creek, fidelity of *Fundulus heteroclitus* to creeks where individuals were originally tagged, and if fish caught outside study creeks moved back into them. The first sampling approach involved using a Visible Implanted Elastomer (VIE) batch tag (Northwest Marine Technology, Shaw Island, WA) to efficiently mark a high number (> 100) of adult fish (≥ 41 mm TL) within each creek over two high tide periods (two batches of tagged fish per creek) in summer 2016. Subsequent minnow trapping in salt marshes over a distance away from creek mouths to a published linear home range of *Fundulus heteroclitus* (200 m) (Skinner et al. 2005) over 3-hour soak times was conducted over low tides over the next month to determine dispersal distances. Low tide is when movement out of intertidal salt marsh creeks is highest for adult *Fundulus heteroclitus* (Allen et al. 2007); the spatial extent of this movement was used to define the effective study areas.

The second type of auxiliary sampling was used to determine whether *Fundulus heteroclitus* emigrates from study creeks to neighboring salt marsh creeks. This emigration, if permanent, would lead to underestimating Φ relative to the latent rate, S . This sampling approach involved high tide minnow trapping (3-hour soak times) to recapture the VIE-

tagged fish (described above). High tide should be a period over which this species is most likely to display fidelity to home creeks based on its use of intertidal salt marsh habitats (Teo and Able 2003; Allen et al. 2007; Rudershausen et al. 2014). Minnow trap recapture effort (3-hour soak times) occurred simultaneously in each study creek and its nearest neighboring creek(s) over three separate high tides that were one, four, and ten weeks after VIE tagging in summer 2016.

The third auxiliary sampling approach was conducted to determine whether PIT tagged fish that were captured outside a creek were resighted within creeks again (i.e. were permanent emigrants). This low tide minnow trapping (on 3 h soak times) outside of creek mouths took place from April through July, 2013. We then examined the antenna detection and physical recapture histories to determine the proportion of individuals captured outside of creeks that were subsequently resighted by the array within each creek.

Estimating apparent survival, detection probability, and density Apparent survival (Φ) and detection probability (p) of PIT tagged *Fundulus heteroclitus* were estimated using a hierarchical formulation of the Cormack-Jolly-Seber (CJS) model fitted in a Bayesian framework. This version of the CJS model has in its likelihood component a state process (whether a tagged individual is alive at sample time i) and an observation process conditioned on state (whether an individual is observed given that it is alive) (Royle 2008; Kéry and Schaub 2012) (Appendix B).

The number of occasions over which CJS model fitting occurred differed among creeks and years. However, we matched the seasonal timing of the start of tagging and the end of monitoring as closely as possible among creeks and years; we commenced tagging in April in each creek and used resight data collected through October 31st for each creek-year

combination (Table 5.2). An occasion was defined as a regular time interval over which a PIT tag receiver was operating and receiving information from the array. One occasion consisted of one day in most cases. A vector containing the number of days per occasion was built into the likelihood portion of the CJS to account for occasions lasting longer than one day. Over those days when a multiplexer was not operational (due to power outages) or when the FS-1001A reader was used (Atlantic Veneer Creek), an occasion was defined as the number of days between operation of the multiplexer or number of days between downloading of the FS-1001A data, respectively.

Both Φ and p were modeled as logistic functions. Each logistic function in preliminary CJS model runs considered occasion-specific- as well as individual fish-specific covariates of both model parameters. Covariates of Φ considered in preliminary models included fish length (upon tagging) and mean water temperature over an occasion. Covariates of p considered in preliminary models included mean water temperature over an occasion and tag size. We assigned uninformative uniform prior probability distributions (lower and upper bounds of 0 and 1, respectively) for Φ and p , and a logit transformation on both Φ and p in the logistic models. Each partial logistic regression coefficient was assigned an uninformative normal prior probability distribution (mean = 0, precision = 1×10^{-6}).

Preliminary model runs revealed that water temperature and fish size were not consistent covariates of Φ (modeled estimates of 2.5 and 97.5 credible intervals did not overlap with zero) and water temperature was not a consistent covariate of p . For these reasons, water temperature was not considered further. In contrast, tag size was a consistently positive covariate of p for all creeks/years when two tag sizes were used (see *Results*).

While the CJS model estimates Φ for an occasion regardless of its length of time, we estimated a daily (24 h) Φ value and a cumulative Φ value; cumulative Φ was calculated as the product of occasion-specific Φ values (across all tagged individuals) over the entire sampling season for each creek/year of sampling. The mean daily Φ value across the season was deterministically calculated as the mean of individual daily Φ values. We also calculated a mean value for p for 8.5 and 12.5 mm PIT tags averaged across all occasions for each season within each creek. This customized CJS model allowed for newly tagged individuals to enter the study after the first occasion and accounted for accidental mortalities of tagged fish during recapture events.

A second component of the demographic model (Appendix B) used the general framework of a Lincoln-Petersen estimator to estimate monthly abundance. We used an ad-hoc form of Lincoln-Peterson estimator rather than a Jolly Seber model because of the high numbers of fish captured that could not be uniquely tagged when they were first encountered (new entrants). This estimate of abundance (\hat{N}_i) on sample date i was defined as:

$$\hat{N}_i = \hat{M}_i \frac{n_i}{m_i}$$

where n_i was the total number of fish in recapture sample date i (see adjustment below for individual growth of tagged fish), m_i was the number of tagged fish in recapture sample date i (Begon 1974; Pollock et al. 1990) and \hat{M}_i was the estimated number of tagged *Fundulus heteroclitus* still alive and available for recapture in the study area (at risk) upon the monthly recapture event. Estimates of Φ were used to estimate the number of tagged fish at risk immediately before minnow trap sampling occurred. \hat{M}_i was calculated as the product of the number of fish tagged and the cumulative Φ between marking and the recapture sampling

date for all released batches in each creek with an array. We estimated the fraction of the population that was tagged ('Fraction Tagged:' Appendix B) upon the timing of each monthly recapture event within the model and assigned it an uninformative uniform prior probability distribution (lower and upper bounds of 0 and 1, respectively); the monthly number of recaptures m_i was defined as a binomially distributed variable with probability of success 'Fraction Tagged' while number of captured fish in sample n_i represented the number of trials. Lastly, the monthly value for \hat{N}_i was calculated by dividing \hat{M}_i by the fraction tagged. The areal density was calculated in the model by dividing each \hat{N}_i by the high tide wetted area in each creek. Since 'Fraction Tagged' was a parameter estimated by the model, it was not possible to incorporate the Chapman estimator to reduce bias (Bailey 1951).

The recaptured fish m_i were from a group of individuals tagged earlier in the season that grew before their recapture on date i . However, the size selectivity of minnow traps used to capture n_i fish each month remained constant. Thus, the size distributions of the previously tagged m_i individuals as well as n_i individuals may not completely overlap since smaller fish that were too small to be retained by the minnow trap on the initial tagging date had grown and recruited to the gear. To have values for n_i and m_i be over similar size ranges of fish, we used mean creek-specific growth rates of recaptured individuals (unpublished data) to calculate the size cut off to use for n_i . Thus, estimates of \hat{N}_i are specific to certain sizes for each month and year but ≥ 41 mm TL.

We tested for the possibility of 'trap happiness' and 'trap shyness' (Nichols et al. 1984) in our monthly minnow trap and cast net recapture sampling. We used two-way contingency tests (χ^2 statistic) ($\alpha = 0.05$) to compare the number of tagged:untagged fish

recaptured between these two recapture gears for each creek/year combination when both gear types were used (2012-13).

For each creek with an array and for each sampling season, median estimates of Φ , p , and density and associated 2.5 and 97.5 credible intervals were obtained by running the model through *OpenBUGS* software (version 3.2.1; Spiegelhalter et al. 2010). The model was run using three Markov chains (independent sample sets) that were updated 10,000 times, with a thin rate of 10 and the first 10 percent of updates discarded as a burn-in phase. Convergence of the chains to a stationary posterior distribution was verified by examining trace plots of retained updates for each model parameter (McCarthy 2007).

Relating Fundulus heteroclitus relative abundance to density We examined the relationship between CPUE and estimated density to determine if CPUE could be used as a proxy for density in the creeks with arrays as well as those without them (Pelletier East and Webb Creeks). Traps can saturate and fail to index abundance when there are higher densities of some fish species (Bacheler et al. 2013). The size cutoff used for year- and month-specific estimates of density was also used when calculating CPUE.

The CPUE-density relationship was tested using regression models. Based on plots of raw data, we fitted two different regression models to the data set. These two types of models were a linear model ($CPUE = a + b * Density$) and an asymptotic model ($CPUE = a + b * (1 - \exp^{-c * Density})$). Each parameter of each model had a normal prior probability distribution with mean = 0 and precision = 1×10^{-6} . Models were fitted by calling *JAGS* version 4.0 (Plummer 2015) from *R* (R Development Core Team 2011) using *R2jags* (Su and Yajima 2015) and run with three chains of initial values updated 10,000 times, with a thin rate of 10 and the initial 1,000 updates discarded as burn-in. Convergence was determined

by computing the Gelman-Rubin statistic (\hat{R}) for each model parameter; values $< \sim 1.1$ for this statistic suggest adequate convergence to a stable posterior probability distribution (Gelman 1996). Support from the data between the two models was compared with Deviance Information Criteria (DIC); models < 5 DIC units of each other were considered to have approximately equal support (Spiegelhalter et al. 2002).

Relating demographics to habitat and urbanization factors General linear models (GLMs) were used to examine the relationship between median daily Φ (single estimate per creek per year) and mean monthly relative abundance (CPUE), respectively, and multiple temporal and spatial factors. GLM fitting used logit-transformed median daily estimates of Φ (from each of four creeks) (*qlogis* function in *R*) and natural logarithm-transformed estimates ($\ln(x+1)$) of mean monthly CPUE data (from each of six creeks) to linearize the relationship between dependent and independent factors for respective models.

We measured a variety of habitat and urbanization metrics at the creek and watershed levels to test for their effects on Φ and CPUE. These metrics were watershed imperviousness, percent marsh and creek channel depth (Table 5.1). Details of watershed boundary and impervious surface delineation can be found in Rudershausen et al. (2016). Year was a temporal effect considered in both Φ and CPUE models given the potential for inter-annual variation in demographics while month was an additional temporal factor in relative abundance models due to declining CPUEs during each year of sampling (see *Results*).

We tested for strong correlations ($r > |0.5|$) between candidate model factors. The Pearson correlation coefficient was calculated between pairs of continuous factors while the Spearman correlation coefficient was calculated when one factor was categorical (Zar 1984).

There were no strong correlations for the Φ data set. For the CPUE data set, a strong negative correlation for the CPUE data set occurred between percent marsh and channel water depth. Continuous habitat and anthropogenic factors were first standardized ((individual covariate value - covariate mean) / covariate standard deviation) to increase the efficiency of the Markov Chain Monte Carlo algorithm (McCarthy 2007).

GLMs were fitted using Bayesian methods (Kéry 2010). An uninformative normal prior probability distribution (mean = 0 and precision = 1×10^{-6}) was assigned to the intercepts (*alpha*) term and each partial regression coefficient (*beta*) for each covariate considered in a model (Kéry 2010). Both Φ and CPUE were defined in the likelihood of respective GLMs as normally distributed variables with mean *mu* and precision *tau*.

While there was collinearity for some of the pairs of factors, we ran a GLM with all the factors examined (a full model) and then ran reduced models with one or model factors removed. This approach was taken to identify which specific factors were most important to Φ and CPUE, respectively, even if they were collinear with another factor. Models fitted to Φ and CPUE started with fitting full-factor models first. Reduced models were considered those with one or more factors removed. We simultaneously used two criteria for constructing models and for comparing models. The first criterion was evaluating the 2.5 and 97.5 credible intervals of partial regression coefficients for each factor considered in a model. We removed factors from further testing if their range between values of 2.5 and 97.5 credible intervals broadly overlapped with zero in the full model. We also fitted null (intercept only) models to Φ and CPUE, respectively. In addition to using credible intervals, DIC was also used as a tool for model selection (Spiegelhalter et al. 2002). Weights (w_i) of support of each model were calculated using the formula, $w_i = \exp(-DIC/2)$ (Spiegelhalter et

al. 2002). The proportional weight of each model was calculated by dividing each w_i by the sum of weights across all fitted models in each set.

Each model was fitted by calling *JAGS* software (version 4.0) (Plummer 2015) from *R* using the interface package *R2jags* (Su and Yajima 2015) and run with three chains of initial values updated 10,000 times. Every 10th observation was retained and the initial 1,000 retained updates were discarded as a burn-in phase. Convergence of each GLM was determined by computing a Gelman-Rubin statistic (\hat{R}) for each model parameter; the number of model updates was increased as necessary to achieve a stable posterior distribution for each parameter, indicated by \hat{R} values < 1.1 .

Goodness of fit of each GLM was assessed by computing a sum-of-squares discrepancy measure. This process involves creating a replicate data set using parameter estimates obtained from each probabilistic model fitted to actual data (Kéry 2010). A sum-of-squares calculation between the predicted and observed values was used as a discrepancy (goodness of fit) measure for both the actual and replicated data sets. A Bayesian probability (p) value (Gelman et al. 1996) was then computed as part of each model run. This p-value computes the proportion of instances when the sum-of-squares values for the replicated data set exceeds that for the actual data set; p-values roughly 0.5 suggest adequate model fit while values close to 0 or 1 suggest a poor model fit (Kéry 2010).

RESULTS

Study area boundaries and site fidelity Sampling to determine study area boundaries for each of the four creeks where Φ was estimated suggested limited low-tide dispersal and high fidelity to each creek. Low tide dispersal was confined to the area immediately outside each creek (< 25 m) except for Porters Creek, where batch-tagged fish were recaptured up to 100

m away from this creek mouth. However, no fish were recaptured at low tide in side creeks neighboring each study creek (Figure 5.3). Thus, the effective study area for tagged fish was within Porters creek as well as from 25 to 100 m away from its mouth. High tide recapture sampling to determine fidelity to study creeks found that only one batch-tagged fish was recaptured in a side creek (neighboring Atlantic Veneer) during the course of this sampling (Figure 5.4). Finally, the re-entry rate of PIT tagged fish after they were recaptured outside of creeks was high; 77, 60, 100 and 97% of PIT tagged fish physically recaptured in 2013 outside of Atlantic Veneer, Porters, Pelletier West and Spooners Creeks were subsequently resighted by the detection arrays in these respective creeks.

Antenna resightings and estimates of apparent survival and detection probability A total of 2,449 fish were PIT tagged over the course of the study. Resighting percentages varied between the two PIT tag sizes. A total of 572 out of 1,131 fish (50.6%) tagged with 8.4 mm tags and 1,100 out of 1,318 fish (84.2%) tagged with 12.5 mm tags were resighted at least once after the occasion on which they were tagged. Percentages of tagged fish resighted at least once were 18.8, 62.3, 39.1, and 77.3% for fish with 8.4 mm tags in Porters, Pelletier West, Atlantic Veneer, and Spooners Creeks, respectively. Resighting percentages of fish with 12.5 mm tags were 80.2, 92.1, 76.2, and 86.6% in these four respective creeks.

For each year of monitoring, detection probability (p) varied between tag types and among creeks. Consistent with the differences in resighting percentages between tag sizes, tag size had a positive influence on p for all 12 creek/year combinations when both tag sizes were used (2012-14). For each tag type, mean estimates of p were highest in Atlantic Veneer Creek over each of the three years of resight sampling there and lowest in Porters Creek over each of the four years of resight sampling there (Figure 5.5).

The 2.5 and 97.5 credible interval estimates for apparent survival (Φ) generally overlapped among creeks during each year of the study. However, there was a trend (depending on year) for Porters and Atlantic Veneer Creeks to have lower median daily Φ values as well as lower season-long Φ values than the other two creeks where Φ was estimated (Pelletier West and Spooners Creeks) (Figure 5.6).

Physical recaptures, density estimates, and relating relative abundance to density The number of physical recaptures during monthly minnow trap and cast net sampling in each creek with PIT tagged fish varied from 0 to 17 and was generally less than one percent of the total number caught (Table 5.3). Recapture rates were higher in spring and early summer and declined to near zero by August and September.

For each creek-year combination we found no significant differences between the two recapture gears (minnow traps and cast nets) in the ratios of tagged:untagged fish (Table 5.4). Thus, we found no evidence of trap happiness or trap shyness and combined the recapture data across monthly minnow trap and cast net deployments in each creek to estimate monthly densities.

Monthly density estimates of adult *Fundulus heteroclitus* varied among creeks and years (Figure 5.7). Differences among creeks within each year were generally most pronounced during the first part of the growing season (April-June). For data from the two creeks sampled in 2011, Pelletier West had higher densities than Porters Creek for May and June (Figure 5.7A). In 2012, Atlantic Veneer and Pelletier West Creeks generally had the greatest densities but credible intervals about these estimates generally overlapped with the other two creeks (Figure 5.7B); a similar trend occurred in 2013 but with less overlap between Porters Creek and the other three creeks early in 2013 compared to a similar period

in 2012 (Figure 5.7C). Porters Creek generally had the lowest densities among the four creeks in both 2012 and 2013.

The relationship between mean monthly minnow trap CPUE and estimated density was linear at low densities but began to asymptote at higher densities (Figure 5.8). However, the asymptotic model fit had a DIC value only 1.0 units less than the linear model (Figure 5.8). Thus, we found evidence for a linear relationship between CPUE and density over the range of these data.

Relating demographics to habitat and urbanization factors We found no evidence that temporal or spatial metrics influenced median estimates of daily Φ . DIC scores for models with individual covariates showed that no model had substantially stronger support than the null (intercept-only) model. Moreover, the 2.5 and 97.5 credible intervals of each covariate considered in GLMs fitted to Φ estimates (year, percent marsh, percent watershed imperviousness, and channel depth) overlapped with zero (Table 5.5).

In contrast to models fitted to Φ estimates, month and percent marsh were important covariates of *Fundulus heteroclitus* CPUE. DIC values and credible intervals not overlapping with zero supported a model with month and percent marsh in a model (Table 5.6). CPUE varied negatively with the progression of sampling season (month) and varied positively with the percentage of each creek's high tide area that was marsh (Figure 5.9).

GLMs fitted to Φ estimates as well as to CPUE data showed convergence to stable posterior probability distributions for the parameters estimated in each model. Additionally, Bayesian p-value estimates suggested good model fits to these data with these each of these p-values being ~ 0.5 (Tables 5.5 and 5.6).

DISCUSSION

Estimating demographic rates of estuarine nekton extends the understanding of how fish respond to habitat and urbanization metrics compared to simply collecting data on species presence/absence (Able 1999). PIT tags and autonomous resighting gear were used to determine survival and abundance of a dominant salt marsh fish and relate them to creek- and watershed-level habitat features along a segment of the rapidly developing U.S. South Atlantic coast. We selected *Fundulus heteroclitus* for study due to its high fidelity to tidal creeks, localized recruitment and movement patterns, and its use as a bio-indicator (Weis et al. 2001; Roling et al. 2004) so that demographic responses could be attributed to patterns and processes operating over localized spatial scales.

The state of North Carolina has assumed in its coastal habitat protection plan and selection of strategic habitat areas that anthropogenic costs lead to reduced fish production (Street et al. 2005). For populations of *Fundulus heteroclitus* in first-order tidal creeks, our results agree with this assumption. Apparent survival was consistent among creeks of varying habitat quality but CPUE (a proxy for density) decreased with lower percentages of marsh. Creeks with the lowest marsh percentages were also systems with less marsh downstream. Salt marsh is a natural resource target identified in the process of selecting strategic habitat areas and elimination of marsh habitats is a cost layer in this process.

Daily and season-long Φ rates were largely consistent among the four creeks possessing PIT tag detection arrays. Minor variation that did exist in Φ rates among creeks was not explained by habitat or anthropogenic factors. Minnow trap sampling to recapture batch-tagged *Fundulus heteroclitus* showed that the effective downstream extent of the study area for these four creeks was roughly the mouth of each creek. These data also showed that

emigration was limited to an area outside each creek but mostly temporary in nature and thus likely to have only a minor influence on estimates of Φ (Williams et al. 2001). Thus, rates of permanent emigration from study creeks were low or zero. As such, estimates of Φ can be considered close to- or equal to rates of true survival (S) for each creek where Φ was estimated.

We believe that low rates of apparent survival in this study are largely from natural sources (e.g., predation) rather than human removals. There are at least two lines of evidence for this. First, very little minnow trap bait fishing for this species was observed in any creek. Second, the creek where no bait fishing was ever observed (Porters Creek) had among the lowest daily and season-long Φ values over each year of the study.

To our knowledge this is the first study to have estimated salt marsh fish demographics in multiple systems and related estimates to landscape-level habitat and anthropogenic effects. In contrast to model fitting to estimates of Φ , models fitted to CPUE data revealed that the relative abundance of *Fundulus heteroclitus* was lower in creeks that had lost components of a natural marsh mosaic. Higher CPUEs were associated with higher percentages of marsh area; these were the study systems that also had the greatest amounts of fringing marsh and greatest percentages of downstream marsh. Creeks with more shoreline armoring, deeper water, and loss of connectivity downstream were associated with lower CPUEs. These latter factors represent common anthropogenic impacts to tidal creeks along the U.S. Atlantic and Gulf of Mexico coastlines (Holland et al. 2004; Sanger et al. 2013; Rudershausen et al. 2016). Results from model fitting underscore the importance of salt marsh as habitat for *Fundulus heteroclitus* forage, refuge, and reproduction (Kneib 1997; Teo and Able 2003).

Localized recruitment and movement patterns of *Fundulus heteroclitus* (Teo and Able 2003; Meyer and Posey 2014) along with results of model fitting indicate that varying abundances among creeks reflect localized habitat and urbanization factors rather than larger-scale (estuary-wide) conditions. Given similar Φ among creeks and limited movement outside creeks, differences in adult abundances among creeks are likely driven by differences in numbers of recruits produced in-stream due to differing percentages of creek-wide marsh surface. Research conducted as part of Chapter 6 tests this hypothesis.

Percent watershed imperviousness was an anthropogenic factor tested in models fitted to CPUE data. Watershed imperviousness is viewed as a composite metric negatively affecting the density and diversity of nekton in freshwater (Wang et al. 2001) and estuarine environments (Holland et al. 2004). Reduced abundances of some tidal creek nekton have been found when watershed imperviousness exceeds 20-30% (Holland et al. 2004); three of the watersheds in which we worked met or exceeded this threshold imperviousness value (Table 5.1). While we worked in a limited number of watersheds, our data suggest that watershed imperviousness did not relate to survival or abundance of *Fundulus heteroclitus*. Further examination of this possibility in other coastal systems and with other nekton species is warranted.

As is the case with estimates of Φ , there are few published estimates of densities of adult *Fundulus heteroclitus* despite the fact that this species is an integral component of tidal creek nekton assemblages along the U.S. Atlantic coast. Comparisons of densities with the few other studies must be made with caution because some estimates were made over different tides, months, or using different sampling gears than ours. Additionally, differences in life stages over which density estimates are made could contribute to discrepancies among

studies. Two high tide density estimates of adult and large age-0 *Fundulus heteroclitus* (reviewed by Teo and Able 2003) are roughly comparable to the high-tide density estimates from this study. Valiela et al. (1977) estimated a mean of 3.1 individuals m⁻² over high tide wetted area in Massachusetts salt marshes while Teo and Able (2003) estimated a mean density of 2.9 individuals m⁻² over high tide in a New Jersey salt marsh. In contrast, we found a mean density of 0.44 individuals m⁻² (S.D. ±0.78) across the four creeks where absolute densities were estimated in this study. While our study estimated densities of *Fundulus heteroclitus* > 40 mm TL, Teo and Able (2003) estimated a mean density for both adults caught by minnow traps as well as large (~ 20-40 mm TL) age-0 fish caught by throw traps. This latter size group comprised a substantial proportion of the catch in some months in that study but was not a size group that our gear selected for in this study, thus could have contributed to density differences between these two studies. Valiela et al. (1977) recaptured tagged adults by deploying minnow traps at constriction points on ebb tides as fish egressed from the marsh. That sampling strategy coupled with potential trap shyness by individuals that Valiela et al. (1977) tagged earlier the same day (due to recovery from the tagging procedure, which would bias density estimates high) may have contributed to differences in mean densities between that study and ours. Finally, our density estimates in four creeks accounted for the full high tide wetted areas in these creeks but a substantial percentage of the high tide area in some creeks (Table 5.1) was comprised of non-vegetated mud bottom, a poorer high tide habitat than marsh for adult *Fundulus heteroclitus* (Hettler Jr. 1989; Teo and Able 2003; Allen et al. 2007). This sampling protocol we employed would theoretically lead to reduced densities relative to studies that sampled exclusively in the marsh, the preferred habitat of this species (Kneib 1997).

Study caveats-There are advantages to using PIT tags to study fish demographics, including the precision obtained in estimating some demographics (e.g., Φ) when using PIT tags in combination with autonomous resighting gear (Hewitt et al. 2010; Rudershausen et al. 2014). However, there are also disadvantages to using PIT tags to study tidal creek nekton. These include the expense, maintenance, construction, and permitting issues for detection arrays, which limited our research to a relatively small number of creeks. Having additional arrays in creeks largely lacking marsh may have revealed lower Φ rates than we found in the four creeks in which we did work, which all had high percentages of marsh cover (> 50%). Survival across numerous salt marsh nekton species has been found to be significantly higher in marsh than non-vegetated areas (Minello et al. 2003).

The CJS model has a number of assumptions (Williams et al. 2001) which, if violated, can bias estimates of Φ . Violation of these assumptions in this study could have led to inaccurately estimating the number of tagged fish at risk and associated density estimates. A violated CJS assumption in this study was that sampling (resighting) is brief relative to the duration of each occasion and that emigration of tagged individuals from a study area is permanent. The autonomous PIT tag detection gear collected resighting data continuously within each occasion; any resighting of an individual within an occasion was used for model fitting. However, Hargrove and Borland (1994) believed that CJS parameter estimates are not badly biased by violations of this assumption. Temporary emigration appears unlikely given our data but if it occurred to and from nearby creeks, it would not bias estimates of Φ if it was random (individuals leaving and returning on a continual basis) (Williams et al. 2001).

The combined approach using resight data along with physical recapture data to inform density estimates has additional assumptions beyond those of the CJS model. One

assumption is that the more frequent resight sampling covers the entire spatial range of the population (Barker 1997). While we used stationary arrays, the number of occasions when resight data were used as well as regular *Fundulus heteroclitus* movement past the arrays (Rudershausen et al. 2014) effectively resighted tagged fish between occasions when mark-recapture gears were used. The combined approach also assumes that fish have the same risk of recapture over successive sampling events (Barker 1997) and that the probability of survival does not depend on a fish's location within its range. However, the small home range (Lotrich 1975; Meredith and Lotrich 1979; Teo and Able 2003) and high site fidelity of this species (Lotrich 1975; Sweeny et al. 1998; Skinner et al. 2005; this study) increases the probability that tagged individuals were available for recapture inside each of the creek areas where trapping and cast netting were conducted.

Unexamined habitat, physical, or chemical factors may have contributed to differences in densities among creeks. For example, salinity can be important in structuring nekton communities in estuaries along the U.S. South Atlantic coastline (Cicchetti 1998; Sanger et al. 2013). However, in contrast to habitat and urbanization factors, it is unlikely that salinity, temperature, and dissolved oxygen significantly affected differences in *Fundulus heteroclitus* densities among the six study creeks, given overlapping values of temperature, salinity and dissolved oxygen among the six creeks (Rudershausen et al. 2016) as well as the ability of this species to tolerate wide ranges of temperature (Garside and Morrison 1977), salinity (Garside and Chin-Yuen-Kee 1972) and dissolved oxygen (Wannamaker and Rice 2000; Stierhoff et al. 2003).

Estimating *Fundulus heteroclitus* abundance allowed the opportunity to test if minnow trap CPUE data indexed density of this species. Kneib and Craig (2001) believed

that minnow trap catches would not reliably index true abundance of *Fundulus heteroclitus* over soak times exceeding roughly 1 hour due to high rates of egress over longer soak times. However, CPUE (over 3-hour soak times) and density were linearly related over the full range of values in this study and the relationship did not begin to asymptote until the highest estimated densities, which were in creeks with habitats favored by *Fundulus heteroclitus*. Having relatively low CPUE values at high densities of this species would only strengthen our findings about habitat features important to it. We conclude that CPUE over 3-hour soak times reliability indexes absolute abundance in salt marsh systems.

Research recommendations Precision about density estimates found in this study could be improved with the recapture of more tagged fish. This could have occurred through two methods: more intensive recapture effort and/or tagging more fish. Batch tagging is a cheaper and more rapid method of marking than surgically implanting PIT tags in anesthetized *Fundulus heteroclitus* (Skinner et al. 2006). For researchers strictly interested in estimating abundance of tidal creek nekton, applying a batch mark to a larger number of animals coupled with recapture sampling shortly thereafter after allowing for mixing due to tides (~ 24 h) would allow for potentially more precise estimates of absolute abundance (density) and reasonably satisfy the assumption of population closure assumed with the Lincoln-Petersen estimator. In addition to using a batch mark to increase precision about abundance estimates, the simultaneous use of PIT tags would assure high precision about Φ estimates relative to more traditional techniques to estimate survival (Hewitt et al. 2010).

PIT tag size and antenna array configuration influenced CJS detection probability. Within each creek fewer fish with 8.4 mm PIT tags were detected by each array than those with 12.5 mm tags. We used 8.4 mm tags to estimate demographic parameters of smaller

fish (< 60 mm) that could not have been successfully implanted with 12.5 mm tags. This study indicates that 8.4 mm PIT tags will prove useful for resighting small *Fundulus heteroclitus* and other small-bodied nekton to estimate their survival in saltwater environments when the detection ('read') ranges can be increased.

The results emphasize the need to estimate multiple demographic parameters when testing for anthropogenic impacts to estuarine nekton. *Fundulus heteroclitus* apparent survival was consistent among creeks with different instream and watershed-level habitat attributes. However, densities differed among creeks. Densities of this species can be expected to decline with increasing urbanization of tidal creeks along the U.S. South Atlantic coastline. These results about the value of salt marsh should provide guidance to natural resource planners charged with attempting to slow the loss of this critical habitat along the rapidly developing U.S. South Atlantic coast.

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Table 5.1. Values for creek- and watershed-level habitat and anthropogenic factors within the sampled area, and the percentage of fringing marsh downstream for six tidal creeks in coastal North Carolina in which demographics of *Fundulus heteroclitus* were estimated.

Creek	Watershed area (m ²)	Impervious area (m ²)	Watershed impervious %	High tide area (m ²)	Marsh area (m ²)	Instream marsh %	Downstream marsh %	Culvert presence	Channel depth (m)
Porters	1,095,729	110,166	10.0	15,162	9,498	62.6	100	No	0.27
Atlantic Veneer	414,224	64,322	15.5	5,209	4,247	81.5	91.0	Yes	0.21
Pelletier West	698,413	325,629	46.7	5,427	3,706	68.3	34.5	Yes	0.28
Spooners	490,859	64,220	13.0	7,691	6,324	82.2	37.3	Yes	0.29
Pelletier East	1,127,387	260,740	23.1	4,170	113	2.7	0	Yes	0.96
Webb	86,951	20,074	23.1	13,494	0	0	0	No	2.00

Table 5.2. Chronicle of mark-resight and mark-recapture sampling events in four salt marsh creeks in coastal North Carolina equipped with autonomous antenna arrays to detect PIT-tagged *Fundulus heteroclitus* from 2011-14.

Year	Creek	Event	Date	Occasion	Comments
2011	Porters	Marking and first day resighting	Apr 14	1	Tagged 53 fish with 12 mm tags
		Marking	May 9	26	Tagged 21 fish with 12 mm tags
		Marking	May 10	27	Tagged 149 fish with 12 mm tags
		Receiver malfunction	May 11-16	-	No resight data collected
		Recapture	May 17	28	
		Receiver malfunction	Jun 6-23	-	No resight data collected
		Receiver malfunction	Jun 25-27	-	No resight data collected
		Recapture	Jun 28	49	
		Receiver malfunction	Jun 29 – Jul 1	-	No resight data collected
		Receiver malfunction	Jul 3-13	-	No resight data collected
		Recapture	Jul 14	51	
		Receiver malfunction	Jul 15-20	-	No resight data collected
		Receiver malfunction	Jul 22-31	-	No resight data collected
		Receiver malfunction	Aug 2-7	-	No resight data collected
		Recapture	Aug 8	54	
		Receiver malfunction	Oct 1-2	-	No resight data collected
		Last day resighting	Oct 31	97	
		Pelletier West	Marking and first day resighting	Apr 13	1
	Recapture		Apr 28	16	
	Receiver malfunction		May 11		No resight data collected
	Marking		May 21	38	Tagged 50 fish with 12 mm tags
	Recapture		May 30	47	
	Receiver malfunction		Jun 1-2		No resight data collected
	Receiver malfunction	Jun 9		No resight data collected	
Receiver malfunction	Jun 13		No resight data collected		
Recapture	Jun 28	72			
Receiver malfunction	Jun 29		No resight data collected		
Recapture	Jul 12	85			

		Receiver malfunction	Jul 13		No resight data collected
		Receiver malfunction	Jul 27		No resight data collected
		Recapture	Aug 17	119	
		Receiver malfunction	Aug 27		No resight data collected
		Recapture	Sep 21	153	
		Last day resighting	Oct 31	193	
2012	Porters	Marking and first day resighting	Apr 12	1	Tagged 46 fish with 8 mm tags Tagged 54 fish with 12 mm tags
		Receiver malfunction	Apr 17-25	-	No resight data collected
		Recapture	Apr 28	8	
		Recapture	May 16	26	
		Recapture	Jun 18	59	
		Receiver malfunction	Jun 27	-	No resight data collected
		Recapture	Jul 10	80	
		Marking	Jul 31	102	Tagged 20 fish with 8 mm tags Tagged 30 fish with 12 mm tags
		Recapture	Aug 4	105	
		Recapture	Sep 17	149	
		Last day resighting	Oct 31	193	
	Atlantic Veneer	Marking and first day resighting	Apr 20	1	Tagged 53 fish with 8 mm tags Tagged 47 fish with 12 mm tags
		No resight data collected	Apr 21-23		
		Recapture	Apr 24	2	
		No resight data collected	Apr 25-30		
		No resight data collected	May 2-6		
		No resight data collected	May 8-15		
		No resight data collected	May 17-20		
		Recapture	May 21	6	
		No resight data collected	May 22-28		
		No resight data collected	May 30-Jun 4		
		No resight data collected	Jun 6-11		
		Recapture	Jun 12	9	

	No resight data collected	Jun 13-21		
	No resight data collected	Jun 23-25		
	No resight data collected	Jun 27-Jul 8		
	Recapture	Jul 9	12	
	No resight data collected	Jul 10-21		
	No resight data collected	Jul 23-29		
	Marking	Jul 30	14	Tagged 47 fish with 8 mm tags Tagged 3 fish with 12 mm tags
	No resight data collected	Jul 31-Aug 4		
	Recapture	Aug 5	15	
	No resight data collected	Aug 6-13		
	No resight data collected	Aug 15-26		
	No resight data collected	Aug 28-Sep 3		
	Recapture	Sep 14	19	
	Last day resighting	Oct 31	66	
Pelletier West	Marking and first day resighting	Apr 12	1	Tagged 69 fish with 8 mm tags Tagged 31 fish with 12 mm tags
	Recapture	Apr 26	15	
	Harvest	May 3	22	Harvested two fish tagged with 12 mm tags (#'s 384.1B7969F6B0 and 384.1B7969F21B)
	Recapture	May 16	35	
	Recapture	Jun 11	61	
	Harvest	Jul 3	83	Harvested one fish tagged with 12 mm tag (# 384.1B7969F31D)
	Recapture	Jul 11	91	
	Marking	Jul 31	111	Tagged 41 fish with 8 mm tags Tagged 9 fish with 12 mm tags
	Recapture	Aug 2	113	
	Recapture	Sep 19	161	
	Last day resighting	Oct 31	203	

	Spooners	Marking and first day resighting	Apr 18	1	Tagged 62 fish with 8 mm tags Tagged 37 fish with 12 mm tags
		Recapture	Apr 27	10	
		Recapture	May 16	29	
		Recapture	Jun 7	51	
		Recapture	Jul 12	86	
		Marking	Jul 31	105	Tagged 32 fish with 8 mm tags Tagged 18 fish with 12 mm tags
		Recapture	Aug 5	110	
		Harvest	Aug 31	136	Harvested one fish tagged with 12 mm tag (# 3D6.000BBD8E5C)
		Recapture	Sep 16	152	
		Last day resighting	Oct 31	197	
2013	Porters	Marking and first day resighting	Apr 18	1	Tagged 100 fish with 8 mm tags Tagged 100 fish with 12 mm tags
		Recapture	Apr 22	5	
		Recapture	May 21	34	
		Marking	Jun 13	57	Tagged 50 fish with 8 mm tags Tagged 50 fish with 12 mm tags
		Recapture	Jun 26	70	
		Recapture	Jul 18	92	
		Marking	Aug 5	110	Tagged 25 fish with 8 mm tags Tagged 25 fish with 12 mm tags
		Harvest	Aug 20	125	Harvested one fish tagged with 12 mm tag (# 384.36F2B3436D)
		Recapture	Aug 27	132	
		Recapture	Sep 18	154	
		Recapture	Oct 21	187	
		Last day resighting	Oct 31	197	
	Atlantic Veneer	Marking and first day resighting	Apr 5	1	Tagged 100 fish with 8 mm tags Tagged 100 fish with 12 mm tags
		No resight data collected	Apr 6 - 15		

	No resight data collected	Apr 17 - 25		
	Recapture	Apr 26	4	
	No resight data collected	Apr 27 - May 2		
	Recapture	May 21	23	
	Marking	Jun 7	40	Tagged 40 fish with 8 mm tags Tagged 50 fish with 12 mm tags
	No resight data collected	Jun 12-13		
	No resight data collected	Jun 16-19		
	Recapture	Jun 20 (19 th)	47	
	Recapture	Jul 23	80	
	No resight data collected	Aug 5		
	Marking	Aug 6	93	Tagged 14 fish with 8 mm tags Tagged 26 fish with 12 mm tags
	Harvest	Aug 20	127	Harvested one fish tagged with 12 mm tag (# 384.36F2B3433D)
	Recapture	Aug 30	117	
	Recapture	Sep 17	135	
	No resight data collected	Sep 18 – Oct 1		
	No resight data collected	Oct 3 – 9		
	No resight data collected	Oct 11 – 18		
	Recapture	Oct 19	138	
	No resight data collected	Oct 20 – 31		
	Last day resighting	Nov 1	139	
Pelletier West	Marking and first day resighting	Apr 3	1	Tagged 100 fish with 8 mm tags Tagged 100 fish with 12 mm tags
	Recapture	Apr 20	18	
	Recapture	May 9	37	
	Harvest	May 9	37	Harvested one fish tagged with 12 mm tag (384.36F2B34239)

		Marking	Jun 6	65	Tagged 50 fish with 8 mm tags Tagged 50 fish with 12 mm tags
		Recapture	Jun 18	77	
		Recapture	Jul 25	114	
		Marking	Aug 8	128	Tagged 25 fish with 8 mm tags Tagged 25 fish with 12 mm tags
		Recapture	Aug 28	148	
		Recapture	Sep 10	161	
		Recapture	Oct 20	201	
		Last day resighting	Oct 31	212	
2014	Spooners	Marking and first day resighting	Apr 16	1	Tagged 100 fish with 8 mm tags Tagged 100 fish with 12 mm tags
		Recapture	Apr 22	7	
		Recapture	May 16	31	
		Marking	Jun 12	58	Tagged 50 fish with 8 mm tags Tagged 50 fish with 12 mm tags
		Recapture	Jun 21	67	
		Harvest	Jun 21	67	Harvested two fish tagged with 12 mm tags and one fish tagged with 8 mm tag (384.36F2B343B2, 384.36F2B341E5, 3D6.001595099D)
		Recapture	Jul 24	100	
		Marking	Aug 7	114	Tagged 27 fish with 8 mm tags Tagged 23 fish with 12 mm tags
		Recapture	Aug 26	133	
		Recapture	Sep 9	147	
		Recapture	Oct 18	186	
		Last day resighting	Oct 31	199	
2014	Porters	Marking and first day resighting	Apr 18	1	Tagged 20 fish with 8 mm tags Tagged 20 fish with 12 mm tags. Tagged 204 fish with fin clip

	Recapture	Apr 30	13	
	Recapture and marking	May 16	29	Tagged 100 fish with fin clip
	Recapture	Jun 11	55	
	Recapture	Jul 10	84	
	Last day resighting	Oct 31	197	
Atlantic Veneer	Marking and first day resighting	Apr 15	1	Tagged 20 fish with 8 mm tags Tagged 20 fish with 12 mm tags. Tagged 204 fish with fin clip
	Recapture	Apr 22	8	
	Recapture and marking	May 12	28	Tagged 100 fish with fin clip
	Recapture	Jun 10	57	
	Recapture	Jul 8	85	
	No resight data collected	Jul 13 – 21		
	No resight data collected	Jul 25 – 28		
	Last day resighting	Oct 31	187	
Pelletier West	Marking and first day resighting	Apr 16	1	Tagged 20 fish with 8 mm tags Tagged 20 fish with 12 mm tags. Tagged 204 fish with fin clip
	Recapture	Apr 21	6	
	Recapture and marking	May 10	25	Tagged 100 fish with fin clip
	Recapture	Jun 8	54	
	Harvest	Jul 4	80	Harvested one fish tagged with 12 mm tag (# 3D9.1C2D6C2481)
	Recapture	Jul 9	85	
	Last day resighting	Oct 31	199	
Spooners	Marking and first day resighting	Apr 17	1	Tagged 20 fish with 8 mm tags Tagged 20 fish with 12 mm tags. Tagged 204 fish with fin clip
	Recapture	Apr 21	5	
	Recapture and marking	May 11	25	Tagged 100 fish with fin clip
	Recapture	Jun 8	53	
	Recapture	Jul 11	86	

No resight data collected	Oct 21 – 23	
Last day resighting	Oct 31	195

Table 5.3. Monthly numbers of recaptured PIT tagged *Fundulus heteroclitus* (m_i) and total numbers captured (n_i) during minnow trap and cast net recapture sampling in four salt marsh creeks in coastal North Carolina from spring through fall, 2011-13. The monthly value for n_i reflects a reduction in the raw monthly n_i value due to mean size increases of recaptured PIT tagged fish in each creek.

Year	Creek	Month	m_i	n_i
2011	Porters	May	28	155
		Jun	22	155
		Jul	16	95
		Aug	3	38
	Pelletier West	Apr	17	105
		May	34	253
		Jun	24	246
		Jul	15	67
		Aug	4	7
2012	Porters	Sep	6	9
		Apr	11	716
		May	3	694
		Jun	2	363
		Jul	0	163
		Aug	0	82
	Atlantic Veneer	Sep	1	29
		Apr	5	1224
		May	10	1421
		Jun	4	579
		Jul	4	2651
		Aug	10	1229
	Pelletier West	Sep	1	522
		Apr	3	283
		May	17	431
		Jun	3	204
		Jul	6	196
		Aug	11	109
Spooners	Sep	0	90	
	Apr	8	806	
	May	16	947	
	Jun	7	321	
	Jul	2	148	
	Aug	1	88	
2013	Porters	Sep	0	36
		Apr	39	901
		May	17	1047
		Jun	34	1035
		Jul	31	925

	Aug	1	33
	Sep	13	178
	Oct	10	194
Atlantic Veneer	Apr	31	1804
	May	20	1450
	Jun	25	1106
	Jul	31	2500
	Aug	12	857
	Sep	3	248
	Oct	7	658
Pelletier West	Apr	21	295
	May	22	1047
	Jun	18	592
	Jul	16	514
	Aug	11	337
	Sep	5	53
	Oct	12	179
Spooners	Apr	99	2344
	May	58	1251
	Jun	72	1080
	Jul	15	212
	Aug	7	111
	Sep	7	90
	Oct	5	82

Table 5.4. Numbers of tagged and untagged *Fundulus heteroclitus* collected by 6.4 mm square wire mesh minnow traps and a 1.2 m diameter, 6 mm mesh monofilament nylon cast net deployed in four salt marsh creeks in coastal North Carolina. For each year/creek combination, a contingency test was conducted (χ^2 test statistic) to determine whether there was a significant difference ($p \leq 0.05$) in the ratio of tagged:untagged fish between the two gear types.

Year	Creek	Minnow trap		Cast net		χ^2	p
		Tagged	Untagged	Tagged	Untagged		
2012	Porters	14	1882	3	371	0	1
	Atlantic Veneer	29	7268	5	1002	0.04	0.843
	Pelletier West	30	968	10	282	0.03	0.864
	Spooners	31	2378	3	108	0.71	0.399
2013	Porters	141	4438	4	64	0.94	0.333
	Atlantic Veneer	119	8124	10	684	0	1
	Pelletier West	101	2888	6	138	0.07	0.785
	Spooners	261	5390	2	112	1.50	0.221

Table 5.5. Bayesian probability values (p), Deviance Information Criteria (DIC) and 2.5, median and 97.5 credible intervals of partial regression coefficients from fitting general linear models to median estimates of daily apparent survival (Φ) of *Fundulus heteroclitus* and time and habitat covariates for four North Carolina tidal creeks. Model #7 is the full model. Model #2 ‘Null’ is the intercept-only model. Δ DIC is the difference between the DIC value for the best fitting model and each model that was fitted. Proportional model weight is w_i . See *Methods* section for a description of covariates and model development.

Model #	Covariate	p	DIC	Δ DIC	w_i	2.5	median	97.5
1	Channel depth	0.548	4.1	0	0.38	-0.954	3.863	8.517
2	Null	0.561	4.6	0.5	0.29	-	-	-
3	Percent imperviousness	0.557	5.8	1.7	0.16	-0.005	0.006	0.016
4	Year	0.566	6.9	2.8	0.09	-0.196	-0.052	0.099
5	Percent marsh	0.562	7.7	3.6	0.06	-0.017	0.001	0.020
6	Year	0.581	10.8	6.7	0.01	-0.213	-0.057	0.107
	Percent marsh					-0.015	0.003	0.022
7	Year	0.548	15.3	11.2	0.00	-0.206	-0.054	0.105
	Percent marsh					-0.013	0.008	0.026
	Percent imperviousness					-0.009	0.003	0.014
	Channel depth					-2.459	3.926	10.677

Table 5.6. Bayesian probability values (p), Deviance Information Criteria (DIC) and 2.5, median and 97.5 credible intervals of partial regression coefficients from fitting general linear models to mean monthly catch-per-unit-effort CPUE data for *Fundulus heteroclitus* and time and habitat covariates for six North Carolina tidal creeks. Model #2 is the full model. Model #6 ‘Null’ is the intercept-only model. Δ DIC is the difference between the DIC value for the best fitting model and each model that was fitted. Proportional model weight is w_i . See *Methods* section for a description of covariates and model development.

Model #	Covariate	p	DIC	Δ DIC	w_i	2.5	median	97.5
1	Month	0.520	234.2	0	0.95	-0.437	-0.331	-0.230
	Percent marsh					0.033	0.039	0.045
2	Year	0.506	239.7	5.5	0.05	-0.296	-0.005	0.307
	Month					-0.438	-0.331	-0.225
	Percent marsh					0.022	0.035	0.047
	Percent imperviousness					-0.021	-0.006	0.009
	Channel depth					-0.938	-0.249	0.410
3	Percent marsh	0.517	266.2	32.0	0.00	0.032	0.039	0.046
4	Month	0.531	326.7	92.5	0.00	-0.516	-0.338	-0.145
5	Month	0.530	332.1	97.9	0.00	-0.525	-0.336	-0.152
	Percent imperviousness					-0.027	0.000	0.027
6	Null	0.509	340.7	106.5	0.00	-	-	-

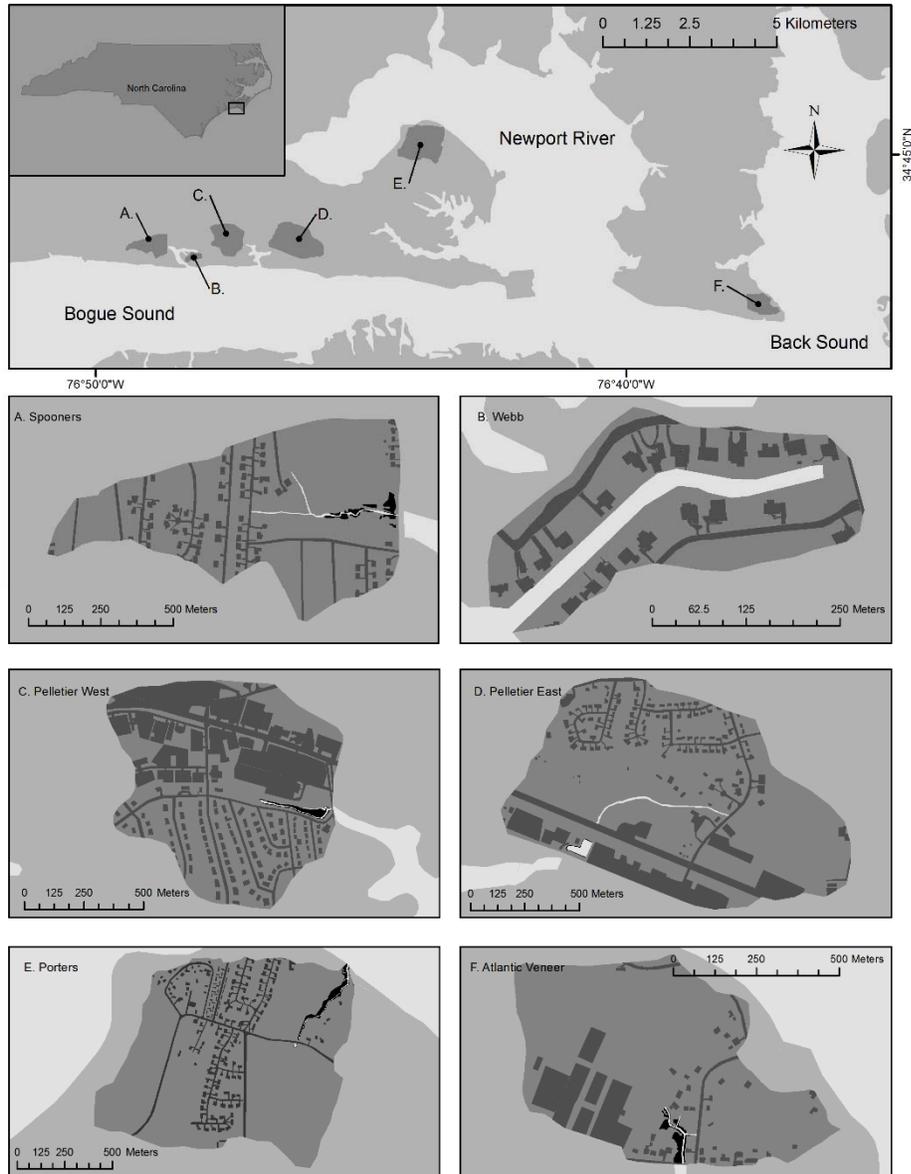


Figure 5.1. Map of six tidal creeks in coastal North Carolina sampled with passive integrated transponder (PIT) tag antennas (all creeks except Webb (B) and Pelletier East Creek (D)) and 6.4 mm wire mesh minnow traps to estimate apparent survival (Φ) and relative abundance of *Fundulus heteroclitus* from 2011-14. Darker shading on the larger inset map represents the watershed of each creek; this is also the gray shade showing watersheds of each creek-specific map. The darkest gray shade for each individual creek map represents impervious surface. The off-white and black in each creek-specific map is the area of the creek channel and marsh surface, respectively.

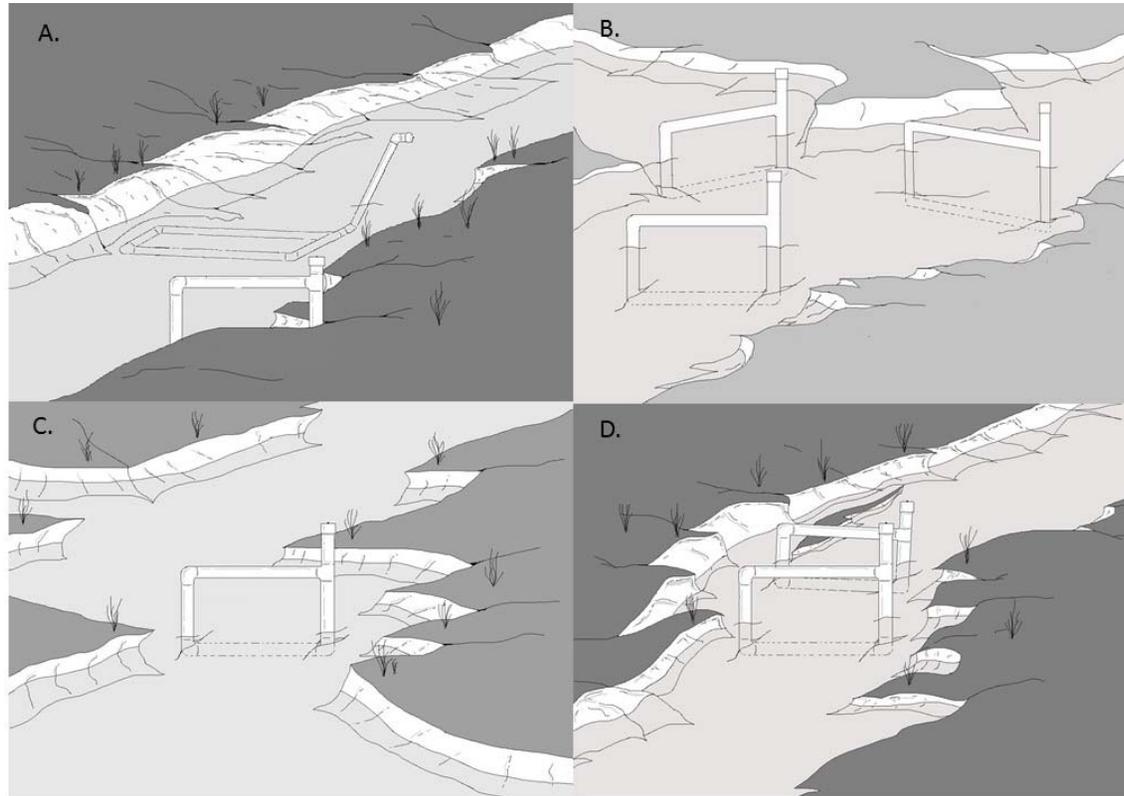


Figure 5.2. Configurations of custom-made antenna arrays used to resight PIT-tagged *Fundulus heteroclitus* in four coastal North Carolina salt marsh creeks. A ‘swim-over’ (horizontal) antenna configuration was used in Porters Creek (A) and ‘swim-through’ (vertical) antenna configurations were used in Porters (A) Pelletier West (B), Atlantic Vener (C) and Spooners Creeks (D).

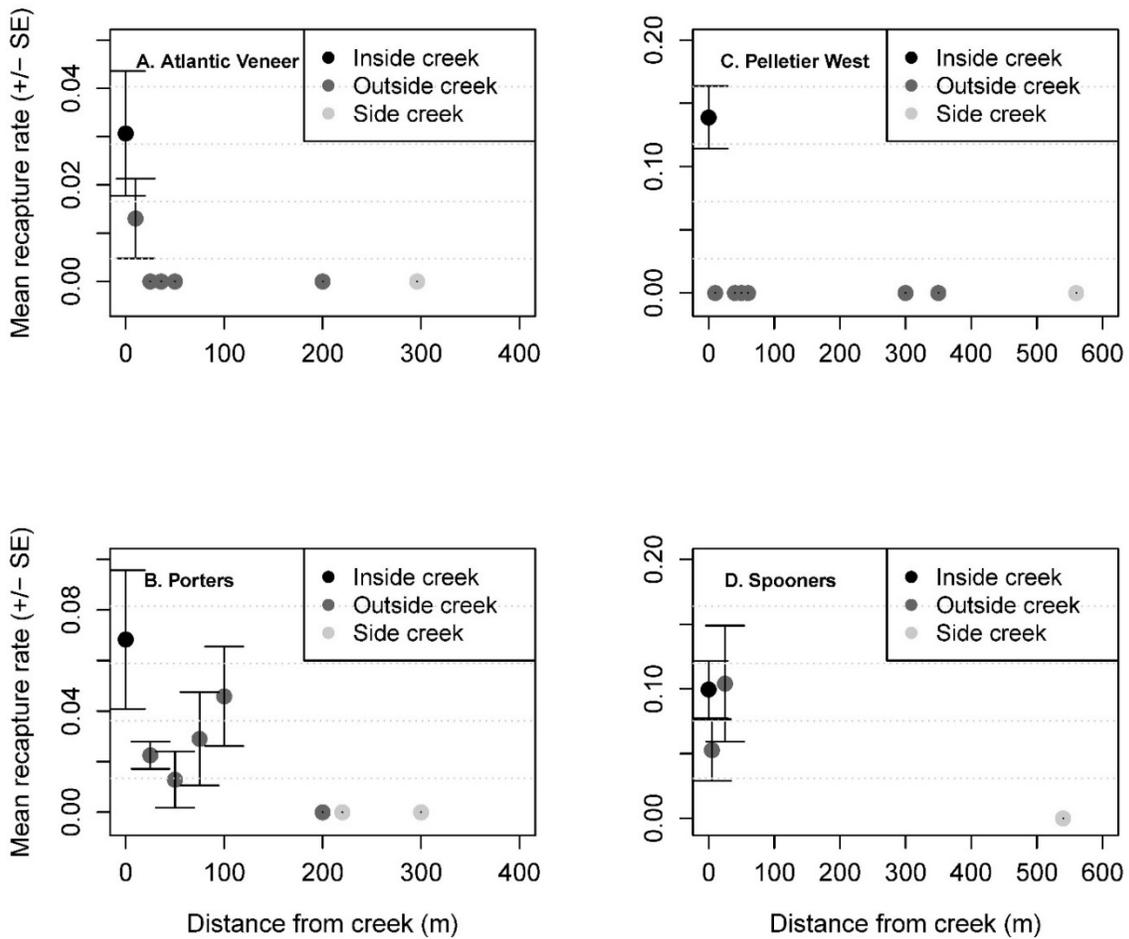


Figure 5.3. Mean recapture rate (catch-per-unit-effort) of batch-tagged *Fundulus heteroclitus* (\pm S.E.) (y axis) vs. distance from the mouth of the study creek (m) (x axis) from minnow trap sampling around low tide inside each of four salt marsh creeks (black symbols), outside each creek (dark gray symbols) and in neighboring side creeks (light gray symbols) in coastal North Carolina in summer 2016.

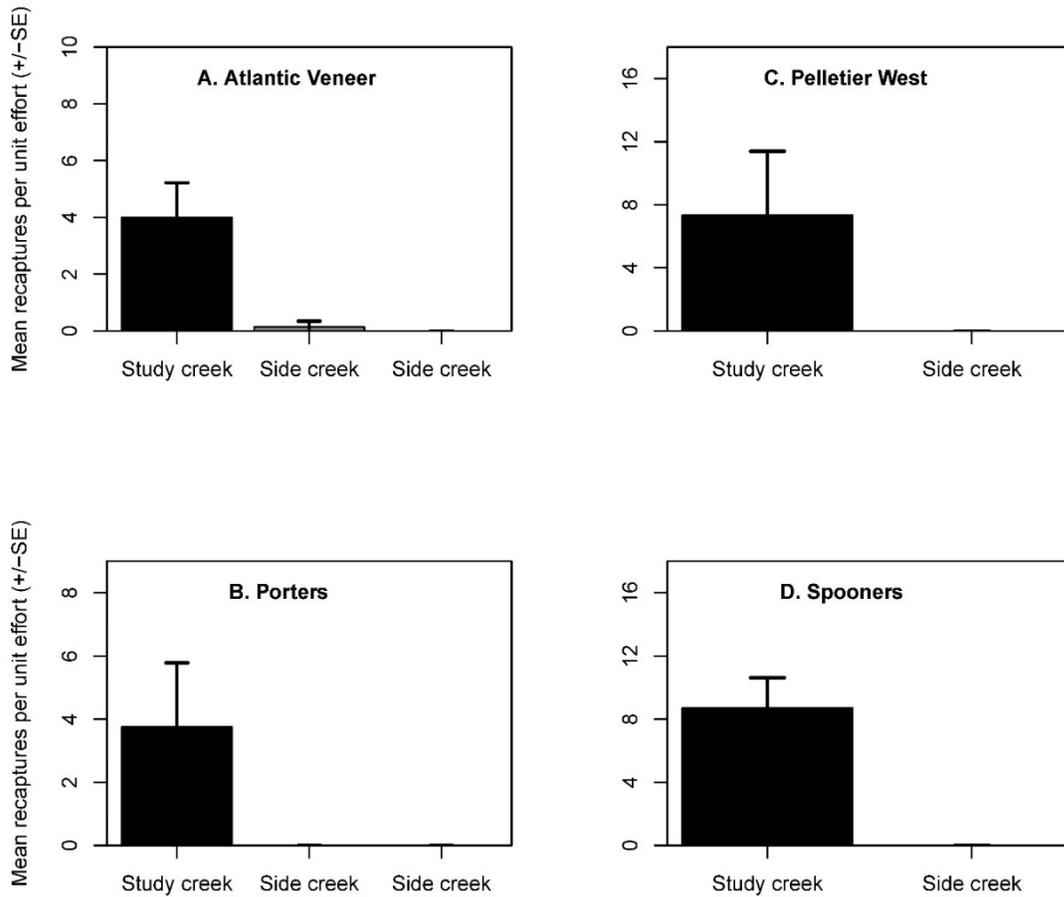


Figure 5.4. Mean recapture rate (CPUE) of batch tagged *Fundulus heteroclitus* (6.4 mm wire mesh minnow traps soaked for 3 hours around high tide) (\pm S.E.) (y axis) in each of four salt marsh creeks (black bars) compared to CPUE in respective neighboring side creeks (gray bars) in coastal North Carolina in summer 2016. Atlantic Veneer (panel A) and Porters Creeks (panel B) had two neighboring creeks each while Pelletier West (panel C) and Spooners Creeks (panel D) had one neighboring creek each. No fish were recaptured in the side creeks respectively neighboring Porters, Pelletier West and Spooners Creeks.

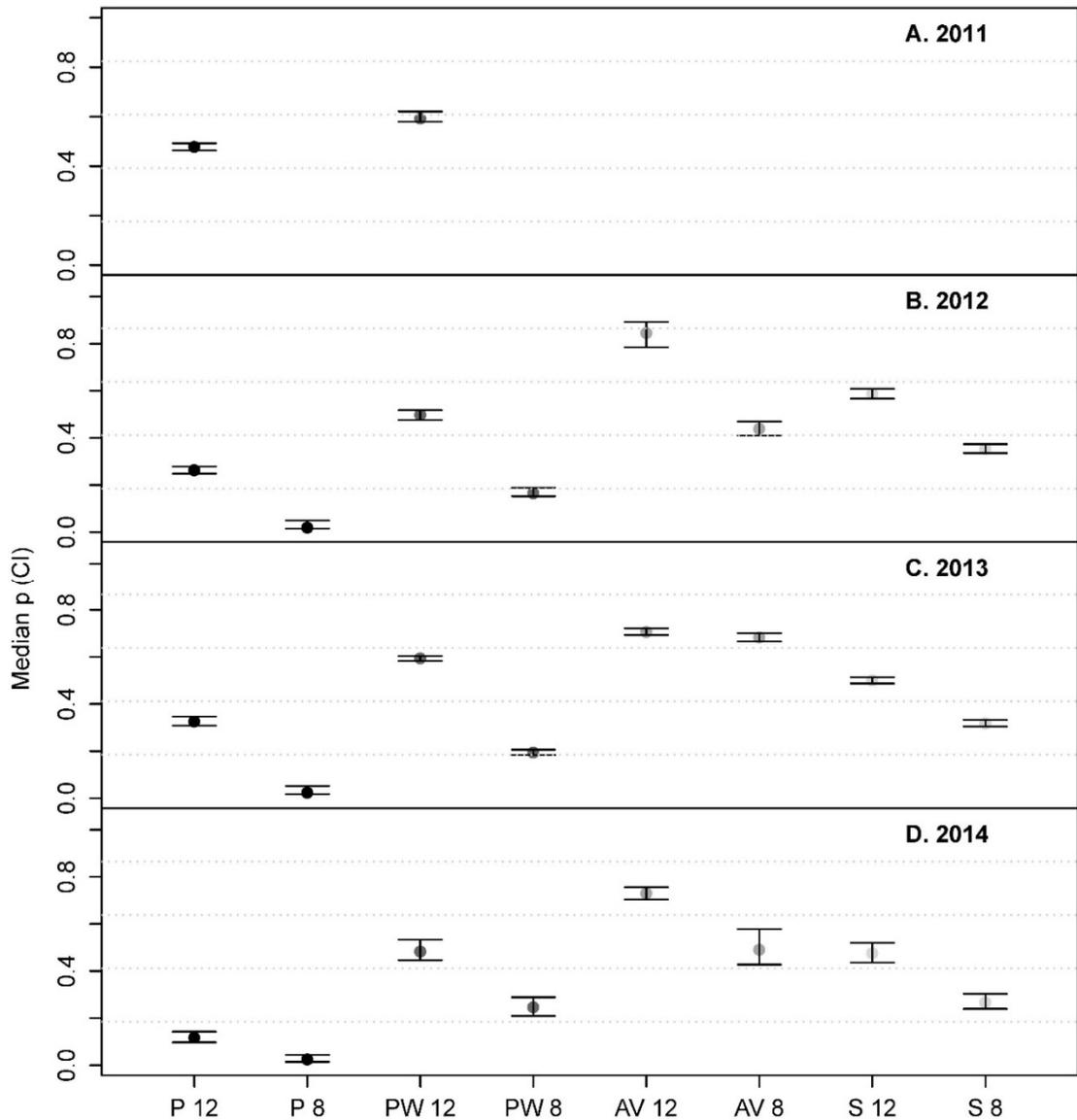


Figure 5.5. Median rates of occasion-specific detection probability (p) along with 2.5 and 97.5 credible intervals (y axis), by creek, from fitting a Cormack-Jolly-Seber model to *Fundulus heteroclitus* mark-resight data. Resight data were collected from spring through fall on fish tagged with 12.5 ('12') mm PIT tags in two North Carolina tidal creeks in 2011 and with 12.5 and 8.4 ('8') mm tags in four creeks in 2012-14. Creek abbreviations: 'P' = Porters, 'PW' = Pelletier West, 'AV' = Atlantic Veneer, 'S' = Spooners.

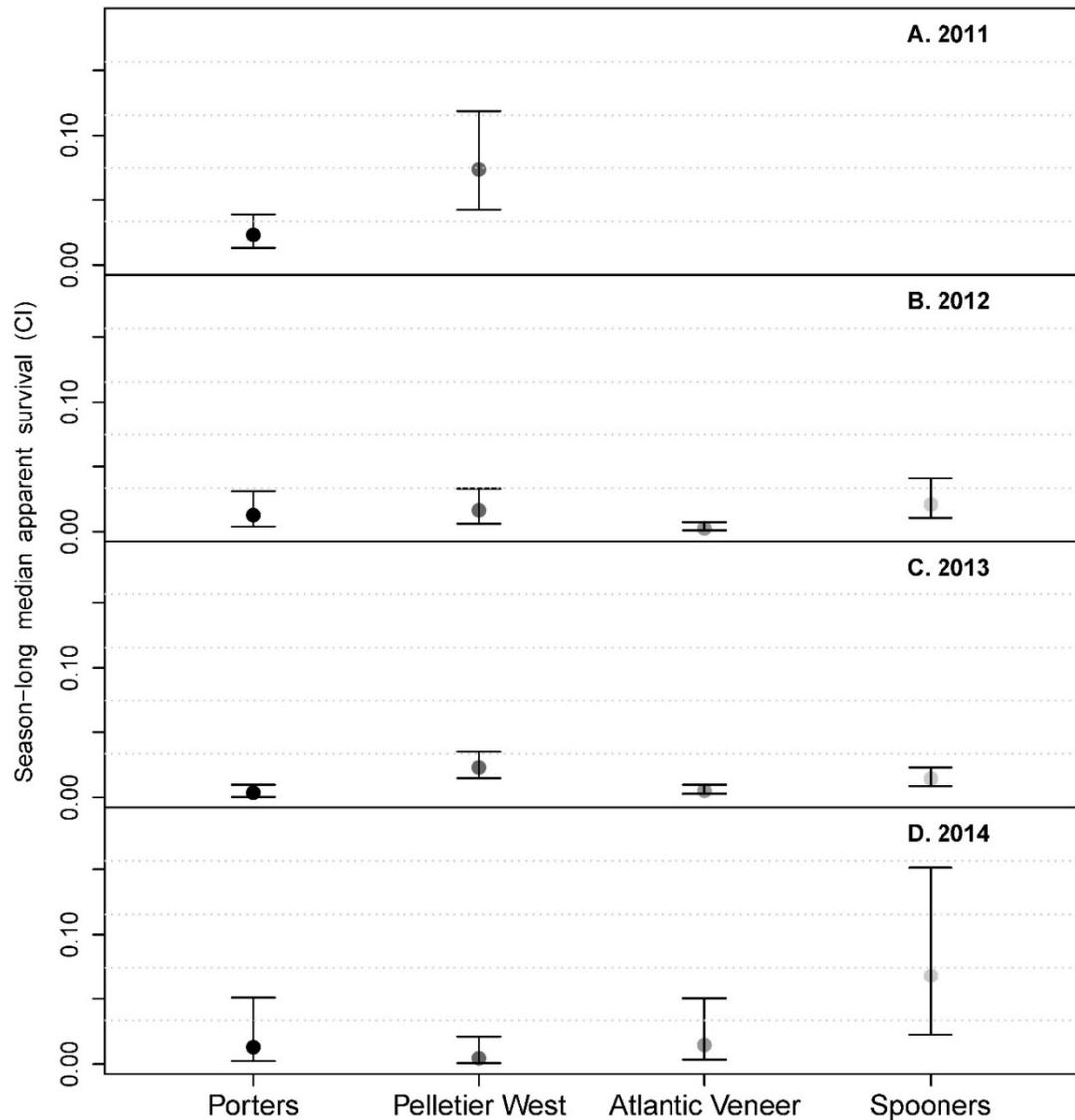


Figure 5.6. Median estimates of overall apparent survival (Φ) (\pm 2.5 and 97.5 credible intervals) (y axis) by creek from fitting a Cormack-Jolly-Seber model to mark-resight data collected from mid-April through 31 October for *Fundulus heteroclitus* tagged in two North Carolina salt marsh creeks with 12.5 mm PIT tags in 2011 (A) and in four salt marsh creeks with 12.5 and 8.4 mm PIT tags from 2012-14 (B-D). Estimates of Φ are across both tag sizes for the three years in which both tag sizes were used (2012-14).

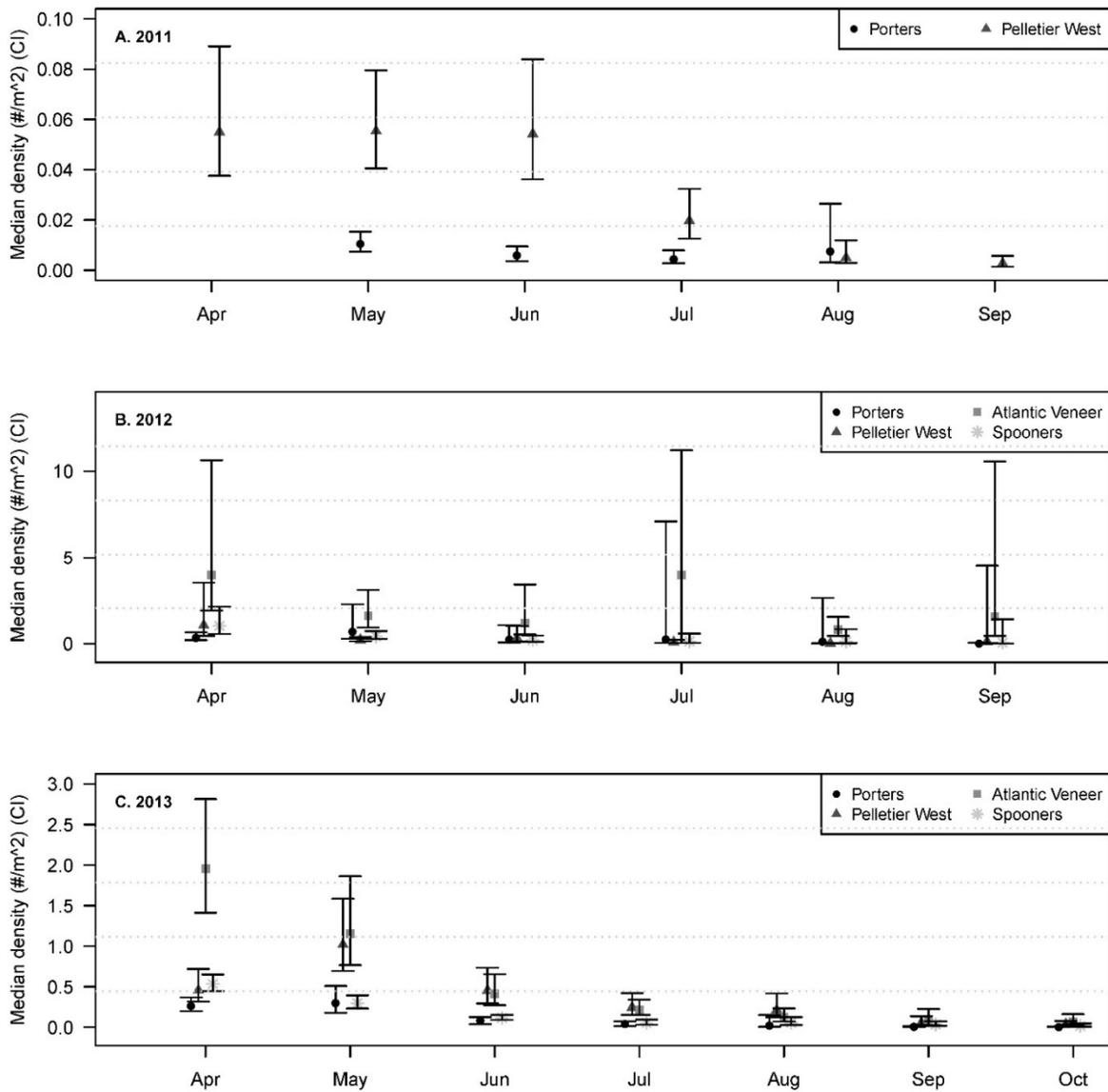


Figure 5.7. Median monthly estimates of high-tide areal density (individuals m^{-2}) (± 2.5 and 97.5 credible intervals) (CI) (y axis) of *Fundulus heteroclitus* in two North Carolina salt marsh creeks in 2011 (A), and in four salt marsh creeks in 2012 (B) and 2013 (C). The range of the y axis differs among panels.

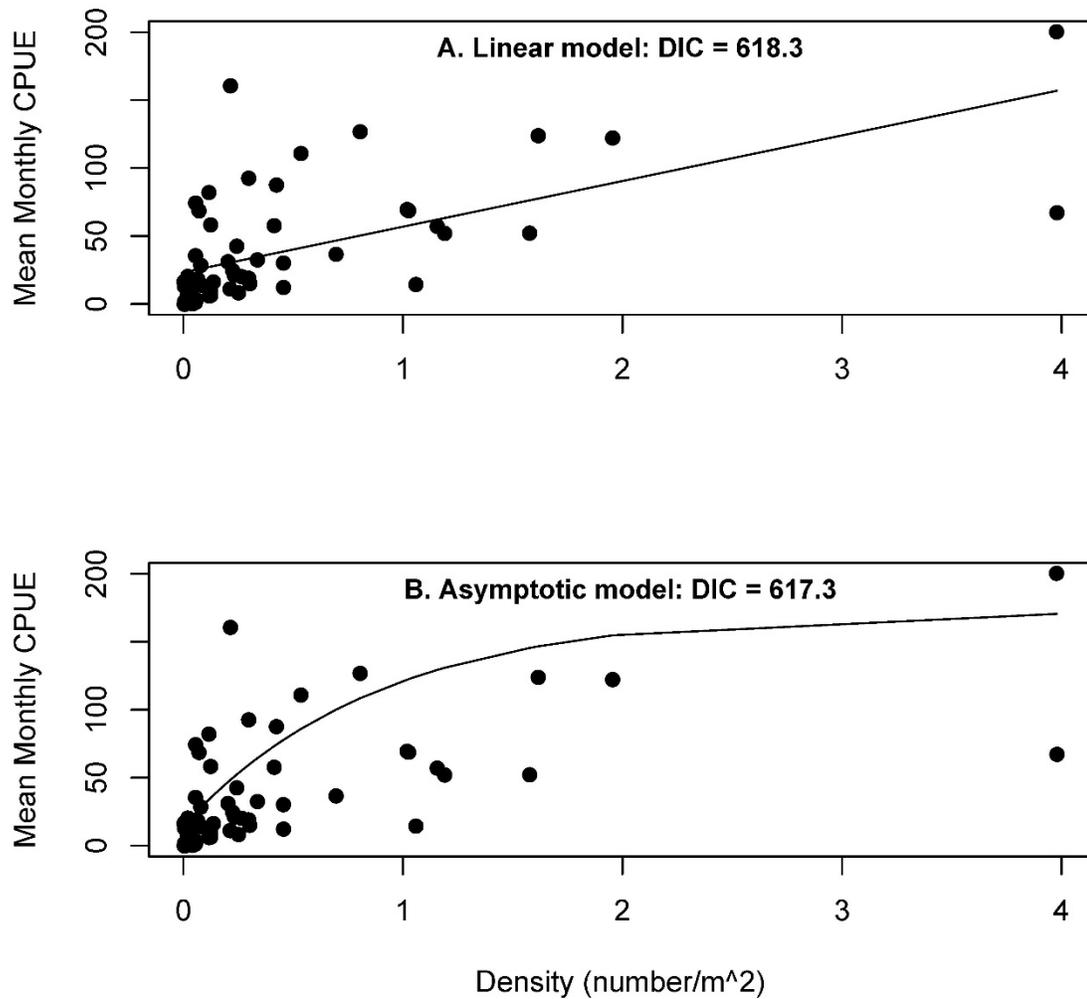


Figure 5.8. Plots of a linear regression model (A) and asymptotic regression model (B) fitted to catch-per-unit-effort (CPUE) data (y axis) and estimated density (individuals m⁻²) (x axis) of *Fundulus heteroclitus* in four salt marsh creeks in coastal North Carolina in 2011-13. The DIC value associated with each model was used to compare parsimony between the linear and asymptotic model fits.

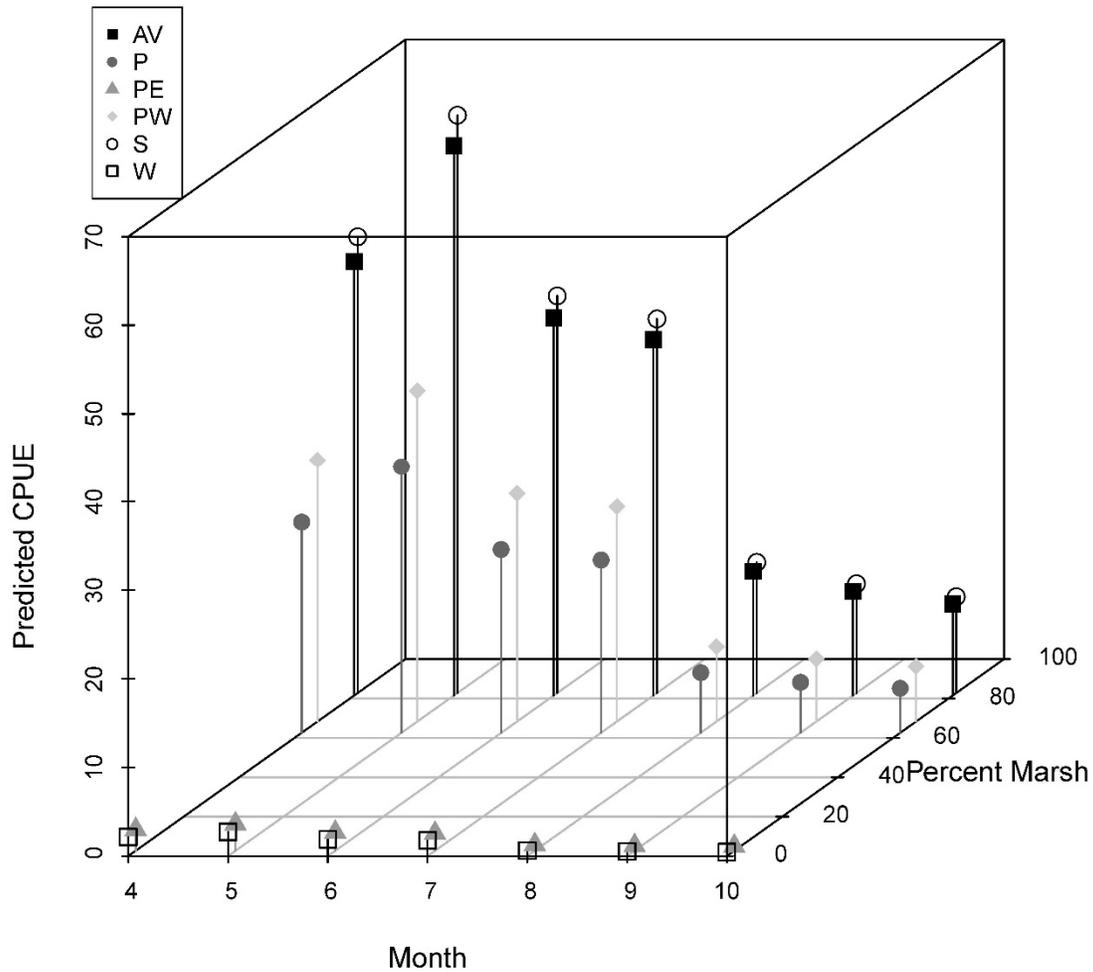


Figure 5.9. Predicted catch-per-unit-effort (CPUE) (z axis) of *Fundulus heteroclitus* vs. month (x axis) and percent marsh (y axis) within the high tide wetted area of six tidal creeks sampled in coastal North Carolina from April through October 2011-13. Predicted CPUE values are from a general linear model with month and percent marsh as explanatory covariates. Creek abbreviations: ‘AV’ = Atlantic Vener, ‘P’ = Porters, ‘PE’ = Pelletier East, ‘PW’ = Pelletier West, ‘S’ = Spooners.

CHAPTER 6. PRODUCTION OF AGE-0 *FUNDULUS HETEROCLITUS* ACROSS A HABITAT GRADIENT IN NORTH CAROLINA SALT MARSH CREEKS

Paul J. Rudershausen and Jeffrey A. Buckel

ABSTRACT

It is unclear how human encroachment in the U.S. South Atlantic coastal zone affects production of dominant tidal creek nekton such as *Fundulus heteroclitus*. We investigated this issue by estimating production of larval and juvenile *Fundulus heteroclitus* in North Carolina tidal creeks. *Fundulus heteroclitus* were collected with a 1 m² throw trap that was deployed in vegetated marsh habitats across a range of landscape-level development intensities in five first-order tidal creeks in coastal North Carolina during the 2012-13 growing seasons. Densities and growth rates were estimated from these data to calculate cohort-specific rates of areal production on the marsh surface. Using general linear models (GLMs) we related areal production on the marsh surface to a variety of factors in order to determine meaningful covariates of production. We then related springtime production extrapolated to high tide wetted areas of creeks to relative abundance of adult *Fundulus heteroclitus* collected in the autumn. GLMs revealed that larval/juvenile production on the marsh surface (g m⁻² d⁻¹) was not related to a composite measure of development intensity - watershed imperviousness - or to the percent of salt marsh within high tide wetted area of creeks. Adult abundance was positively related to larval/juvenile production that was extrapolated to full high tide wetted areas of creeks, indicating that greater creek-wide production of larvae/juveniles as a likely explanation for greater densities of adults in some creeks than others. The results demonstrate the ability of *Fundulus heteroclitus* to maintain within-marsh areal production levels in more heavily developed tidal creeks and their

watersheds as long as critical salt marsh habitat is not removed by instream development types common in this region (e.g., shoreline armoring, dredging, culvert construction).

INTRODUCTION

Estimates of secondary biological production are an indicator of ecological integrity that can be compared among habitats, regions or types of impacts (Mann and Penczak 1986; Able 1999; Randall and Minns 2000; Rakocinski and Zapfe 2005; Hayes et al. 2007). Further, estimates of secondary production are valuable for determining the ability of estuaries to serve as nurseries because they account for density, growth, and mortality (Beck et al. 2001). However, because of the openness of salt marsh habitats (Kneib 2003) and extensive data requirements (Able 1999), production is infrequently estimated in these systems or in estuaries in general. This is unfortunate because important natural and anthropogenic drivers of nekton production are only recently becoming understood for many fish and invertebrate species inhabiting rapidly developing U.S. South Atlantic and Gulf of Mexico estuaries (Partyka and Peterson 2008; Peterson and Lowe 2009; Lowe and Peterson 2014). Furthermore, the relationship between fish production and vegetated habitats, such as salt marshes, is often an important justification for protecting imperiled habitats in regions with rapid coastal development (Kneib 2003; Dahlgren et al. 2006).

Urbanization of salt marsh mosaics – the severing and serial replacement of these habitats with hardened surfaces and shorelines (Lowe and Peterson 2014) – fragments them into increasingly smaller and more isolated patches along the U.S. coastlines (Holland et al. 2004; Bromberg and Bertness 2005; Lowe and Peterson 2014; Sanger et al. 2015) as well as along coasts of other continents (Doody 2004; Duarte et al. 2008; Gedan et al. 2009). Some specific impacts, including habitat fragmentation, shoreline armoring, and dredging, are

implicated for affecting the biotic integrity of nekton populations in estuaries in the U.S. South Atlantic region (Bilkovic and Roggero 2008; Bilkovic 2011; Gittman et al. 2015; Rudershausen et al. 2016). It is in first-order tidal creeks in low-relief coastal areas, by virtue of their proximity to uplands, where the most impacts from development occur (Holland et al. 2004; DiDonato et al. 2009). While landscape-level impacts of development have been implicated for reducing secondary production (Holland et al. 2004; DiDonato et al. 2009), to our knowledge this theory has not been tested along a gradient of impacts in estuaries.

Recognizing anthropogenic encroachment into its estuaries, natural resource managers in North Carolina have stated that more fishery-independent information is needed to help determine natural and anthropogenic drivers of estuarine nekton production (NCDMF 2010; Jensen et al. 2014). Effective fisheries management in estuaries requires information relating fish populations to the usage of habitats targeted for protection by natural resource planners (Skilleter and Loneragan 2003; Dahlgren et al. 2006) and secondary production is a useful measure of ecosystem response to stressors (Mann and Penczak 1986; Able 1999; Valentine-Rose et al. 2007). Work on estimating production and relating it to habitat and anthropogenic factors in estuaries provides timely information to natural resource planners charged with identifying and mitigating anthropogenic threats and protecting critical estuarine habitats.

This study researches production of *Fundulus heteroclitus*, the dominant fish species inhabiting salt marshes along the Atlantic coast. It uses these habitats for foraging, refuge, reproduction and nursery (Kneib 1986; Kneib 1997a). Production of this species in salt marsh habitats has been estimated before. However, the expectation is for production of any one nekton species to vary considerably among estuaries based on habitat quality (Able

1999; Kneib 2003; Krebs et al. 2014), which is a reason why we worked in multiple study systems. This research focused on larval and juvenile age-0 fish because they contribute the majority of production of this species in salt marsh systems (Meredith and Lotrich 1979; Teo and Able 2003a; Hagan et al. 2007). An advantage to estimating production of larvae and juveniles of this species is that they largely remain on the vegetated marsh surface (Kneib 1984; Teo and Able 2003b). Thus, corrections to production estimates to account for immigration and emigration from study creeks (Stevens et al. 2006) are not needed for these life stages.

Previous work in North Carolina salt marsh habitats found that nekton communities differ across a gradient of anthropogenic impacts to salt marshes (Rudershausen et al. 2016; Chapter 2). Adult *Fundulus heteroclitus*, while having similar rates of apparent survival among creeks, have the greatest relative abundances in creeks with the highest percentages of vegetated salt marsh with their high tide wetted areas (Chapter 5). This relationship with vegetated salt marsh could result from higher creek-wide larval/juvenile production of *Fundulus heteroclitus* in creeks with higher percentages of marsh because of the physical importance of marsh for egg deposition and as habitat for subsequently recruited larvae and juveniles.

In this study we estimated larval/juvenile *Fundulus heteroclitus* production in multiple tidal creeks and tested whether it differed as a function of landscape-level habitat and anthropogenic factors. Additionally, we tested for a relationship between larval/juvenile production and subsequent recruitment of adults to elucidate a mechanism behind greater density of adults in some study creeks than others. This project builds on previous studies of *Fundulus heteroclitus* production (Valiela et al. 1977; Meredith and Lotrich 1979; Teo and

Able 2003a; Hagan et al. 2007) in that it works across multiple study areas to test for the influences of natural and anthropogenic factors that may affect nekton production.

METHODS

Study Sites Five first-order tidal creeks in coastal North Carolina (USA) were sampled: Atlantic Veneer, Porters, Pelletier East, Pelletier West and Spooners Creeks. These tidal creeks have habitat and alterations to their high tide wetted areas and watersheds (Table 6.1) that epitomize common residential and commercial impacts to these systems in the U.S. South Atlantic coastal plain (Holland et al. 2004) and the patchiness of estuarine habitats in heterogeneous coastal landscapes (Boström et al. 2011).

Production in intertidal areas, such as salt marshes, depends partly on their physical accessibility to secondary consumers (Kneib 2003); the sampled portions of study creeks are positioned within their respective watersheds such that the duration of marsh flooding from semi-diurnal tides, and thus the temporal accessibility to the marsh surface by nekton, is roughly equal among them (pers. obs). The study creeks are considered polyhaline in that high tide salinities at the downstream ends of sampled areas (at creek mouths or culverts) are roughly 30 psu during dry periods and 10 psu during episodic rains (unpublished data). Atlantic Veneer, Porters, and Spooners Creeks are ‘rivulet’ marsh creeks (Rozas et al. 1988; Hettler 1989) with shallow flows of water (~0.1 m deep at low tide) that meander through part of their channels over low tides. In contrast, the channel of the lower half of Pelletier West Creek is largely covered with water over low tides. Each creek has fringing marsh dominated by *Spartina alterniflora* (Loisel) (Table 6.1). Pelletier East Creek was historically a rivulet marsh creek but now has the narrowest lateral fringing marsh due to being dredged; it is a saltwater pond possessing standing water over all tides. Below their sampled areas

Pelletier East, Pelletier West, and Spooners Creeks have predominantly bulkhead shorelines with essentially non-existent (Pelletier East) or sparse *Spartina alterniflora* coverage (Pelletier West and Spooners).

The delineation of the downstream extent of habitat is often subjective in studies of production within salt marshes (Kneib 2003). Culverts can delineate boundaries of salt marshes (Stevens et al. 2006); we bounded the downstream sampling limit in each creek by the presence of a culvert or the downstream confluence with a higher order estuary. Upstream sampling was bounded by the most upstream extent of tidal influence or, in the case of Pelletier East Creek, an upstream culvert. Thus, except for Pelletier East Creek, each creek was sampled from the downstream mouth or culvert to the upstream extent of tidal influence. Watershed boundaries and watershed impervious surface percentages for each creek were estimated using *ArcGIS* (version 9.3.1). Details of this process can be found elsewhere (Rudershausen et al. 2016).

Field sampling The five study creeks were sampled monthly from April through October of 2012 and 2013 to provide data to estimate production of age-0 larval/juvenile *Fundulus heteroclitus*. These are typically the months over which this species spawns in this general region (Kneib and Stiven 1978; Taylor et al. 1979). Logistics prevented sampling all five study creeks over the same day each month. This would have been ideal since *Fundulus heteroclitus* spawns predominantly over the full and new moons during spring and summer months (Taylor et al. 1979).

Each creek was divided into ten evenly spaced transects; all ten transects (or a lesser number due to tidal levels) were sampled on the same day each month. The sampling gear was a 1.0 m² square, 0.6 m high solid aluminum-framed throw trap that was deployed by foot

on the flooded marsh surface. The throw trap is an areal sampling device useful for targeting small fishes in vegetated habitats (Rozas and Minello 1998; Turner and Trexler 1997). When adjusted for catchability, throw trapping allows estimates of absolute density of nekton (Kushlan 1981; Rozas and Minello 1997; Rudershausen et al. 2016).

For this study the throw trap was used to target small (< 40 mm total length) *Fundulus heteroclitus*. Variation in the frequency and duration of tidal inundation in salt marshes can influence the density of young *Fundulus heteroclitus* on the marsh surface (Kneib 1997b). For this reason the throw trap was deployed over high tides using a stratified random sampling design with respect to distance upstream within each stream transect, left vs. right fringing marsh (facing upstream), and lateral distance into the fringing marsh towards upland. Such a sampling design also accounted for variability in nekton densities with lateral distance away from sub-tidal habitats (Kneib and Wagner 1994; Allen et al. 2007). Ten trap deployments were generally made monthly in each creek except in Pelletier East Creek where the narrowness of the marsh there prevented trap deployment in roughly half of the strata (depending on tidal level). Immediately after deployment the trap frame was pressed into the sediment to prevent escapement of trapped fish. Water depth was measured (± 0.1 m) and percent vegetation (*Spartina alterniflora* stem density) in the trap was visually estimated (nearest 10%) in conjunction with each deployment. We swept each trap deployment 50 times with a 0.30 x 0.25 m dip net possessing 0.72 mm² mesh and initially removed vegetation by sieving each trap's sample through a wash bucket with 0.22 mm² mesh. All fauna and remaining organic matter were preserved in 95% denatured ethanol for later sorting, identification and fish measurement.

Adjusting the length of throw trapped fish and estimating fish dry weights Each preserved throw trap sample was largely composed of detritus. This volume of detritus logistically prevented us from sorting samples while they were fresh. Samples were sorted between 6 and 18 months after collection. Potential shrinkage in fish length due to this time lag was taken into account to more accurately estimate the original fresh lengths of small preserved fish (Cunningham et al. 2000). We also developed dry weight:total length relationships reflective of unpreserved fish since, as with fish lengths, weights of individuals were not recorded upon field collections. Adjustments to fish lengths and estimation of dry weights are described below.

Age-0 *Fundulus heteroclitus* ranging from 8.9 to 42.7 mm total length (TL) were sampled with a dipnet from each creek to investigate the proportional shrinkage over the period between field sampling and sample sorting; these collections were separate from throw trap collections to estimate density for production. Each individual was measured (TL: 0.1 mm) and stored in a uniquely labeled vial containing 95% denatured ethanol, the same preservative used for throw trap samples. Each preserved individual was re-measured at 36, 196, 485, and 673 days after its field collection to encompass the approximate range of times we believed, *a priori*, would be needed to sort throw trap samples. It was found from plotting proportional change in total length against elapsed time that the rate of shrinkage decreased with time (Figure 6.1) and that the slope of a linear regression line fit to shrinkage data measured 196, 485, and 673 days after collection (last three time points) was not significantly different than zero ($p = 0.059$). The mean proportional decrease in length over these three time points was 0.065. Based on this, and because throw trap samples were sorted roughly 6-18 months after collections, we adjusted the length of each preserved

Fundulus heteroclitus in throw trap samples upwards by 6.95% (preserved length x 1.0695). The proportional amount of shrinkage of small fish due to preservative appears to be independent of fish length among a variety of small-bodied fish species (Cunningham et al. 2000); therefore, original fish size was not taken into account when making adjustments to the length of each preserved individual.

Dry weights are often used to estimate production of small bodied fishes, including *Fundulus heteroclitus* (Teo and Able 2003a). Due to the time lag between throw trapping and sample sorting, which prevented obtaining accurate dry weights from freshly collected fish, dry weight-total length relationships were developed for each creek. To develop these relationships, *Fundulus heteroclitus* were collected with a dipnet from each creek. After collection fish were placed on ice and returned to the lab for measurement of unpreserved TL (± 0.1 mm). Fish were then dried for 48 h at 60°C and weighed on a microbalance to obtain dry weight (DW) (± 0.00001 g).

Data on DW and TL were natural logarithm (ln)-transformed to establish a linear relationship between the two variables: $\ln(\text{DW}) = a + b * \ln(\text{TL})$. Each creek-specific linear regression explained a high proportion of variability about the data (adjusted $r^2 > 0.8$). The DW-TL relationship for each creek (Figure 6.2) was then used to estimate the DW of each individual collected from throw trap samples after correcting those lengths due to preservation.

Adjustments to throw trap catches due to recovery efficiency Catch rates of nekton in a throw trap can be biased due to incomplete recovery of all targeted individuals enclosed by the gear (Kushlan 1981; Rozas and Minello 1997). Catchability by a throw trap has two components: capture efficiency and recovery efficiency (Rozas and Minello 1997); capture efficiency is

the proportion of targeted individuals in a physical area that are enclosed by the trap while recovery efficiency is the proportion of individuals recovered relative to those physically enclosed. Given the small size of larval/juvenile age-0 *Fundulus heteroclitus* targeted by the throw trap (<~ 40 mm total length), we were less concerned about capture efficiency than recovery efficiency. The catch from each trap deployment was adjusted for recovery efficiency to estimate absolute density of *Fundulus heteroclitus*. The methods for estimating recovery efficiency by this gear can be found elsewhere (Rudershausen et al. 2016). Briefly, recovery efficiency of *Fundulus heteroclitus* was estimated with a depletion method and efficiency estimates were found to be a function of emergent vegetation (*Spartina alterniflora*) density.

Tracking mean cohort-specific growth of age-0 fish captured by the throw trap Estimating fish production requires information on growth of individuals. For this study, growth data for age-0 larval/juvenile *Fundulus heteroclitus* were obtained by constructing length frequency histograms to track individual cohorts across two successive months of sampling. Monthly length frequency histograms of throw trapped *Fundulus heteroclitus* from each study creek were plotted to identify age-0 cohorts newly recruited to the throw trap as well as estimate growth of age-0 cohorts already recruited to the gear in an earlier month (Figure 6.3). We estimated growth and production on a cohort-specific basis due to the repeated recruitment of new cohorts of fish to the gear over the growing season.

Simple rules were developed to identify and distinguish cohorts of *Fundulus heteroclitus* using length frequency histograms. We used breaks in observations (low numbers of observations per length bin: antimodes) in length frequency histograms as guides in the selection of the range of length of individuals contributing to each cohort in monthly

length frequency histograms (Figure 6.3). More than one captured individual was required to distinguish a cohort from a monthly set of throw trap samples in a creek. Using these criteria, the same number of cohorts was not necessarily equal among creeks within the same month. Additionally, no cohorts were identified for some creek/month combinations. Owing to concerns about capture efficiency being less than 100% and to restrict production to age-0 fish, estimates of production were limited to cohorts that had an average size (across all creeks and cohorts tracked) of 20.5 mm TL. Estimated production in this study was cohort-specific; the inability to lump some individuals into cohorts (Figure 6.3) prevented estimation of cumulative production (summing across all captured age-0 larval/juvenile individuals) for any creek/time period.

Calculating production of throw trapped Fundulus heteroclitus Dry weight production ($\text{g m}^{-2} \text{day}^{-1}$) was calculated for each cohort of throw trapped age-0 larval/juvenile *Fundulus heteroclitus* tracked across two consecutive months. Biological production is the elaboration of tissue over time and thus a function of growth and biomass of a cohort (Ivlev 1945); we estimated production using a method that incorporates the instantaneous growth rate of the cohort of fish being tracked and the cohort's mean biomass over the inter-monthly time period (Ricker 1975). The time period over which production estimates were made was short (~1 month) relative to the approximate one year generation time of this species (Kneib and Stiven 1978) so a linear biomass model (\bar{B} : see below) was chosen over an exponential model (Parsons and Takahashi 1977); this model choice is consistent with previous work on production of *Fundulus heteroclitus* (Valiela et al. 1977; Teo and Able 2003a).

Instantaneous growth rate, G_{inst} , for a cohort and the cohort's mean biomass across successive sampling events was calculated as the mean natural logarithm-transformed (ln)

dry weight of cohort-specific individuals upon the first (\bar{w}_1) and second (\bar{w}_2) of two successive sampling dates, respectively, divided by the time (in days) between the first (t_1) and second (t_2) sampling events:

$$G_{inst} = \frac{\ln(\bar{w}_2) - \ln(\bar{w}_1)}{t_2 - t_1}$$

For this study, calculations of \bar{w}_1 and \bar{w}_2 for a cohort used the mean dry weight value predicted from total lengths of throw-trapped fish upon each sampling date.

Mean biomass of a cohort (\bar{B}) between successive sampling events was the other metric used for estimating production in this study. \bar{B} has two components. The first is density. Mean monthly density of each tracked cohort of larval/juvenile fish in a creek (\bar{N}) was calculated as the average catch of individuals within a cohort across all monthly values of density for each cohort in a creek. These calculations assume that \bar{N} is representative of the mean density over the entire salt marsh surface in a study system (Teo and Able 2003a). The 2.5 and 97.5% confidence intervals (CIs) about \bar{N} in the first month (\bar{N}_1) and second month (\bar{N}_2) in each creek were also calculated. The CIs about density were used to calculate 2.5 and 97.5 CIs for production (Teo and Able 2003a) due to the fact that the principal source of error in estimating production arises from variability about density rather than variability about growth (Chapman 1967; Mann and Penczak 1986; Morin et al. 1987; Teo and Able 2003a). The second component of \bar{B} is the mean estimated dry weight of individuals upon the first (\bar{w}_1) and second (\bar{w}_2) of two successive sampling occasions. \bar{B} is then calculated by the equation,

$$\bar{B} = \frac{\bar{N}_1 \bar{w}_1 + \bar{N}_2 \bar{w}_2}{2}$$

where \bar{N}_1 and \bar{N}_2 as well as \bar{w}_1 and \bar{w}_2 are defined above.

For each tracked cohort, areal production (P) between sampling events in two successive was taken from Ricker (1946; 1975) and Allen (1949) and calculated as,

$$P = G_{\text{inst}} * \bar{B}.$$

As with calculations of \bar{B} , the lower and upper CIs of production were calculated. These CIs capture only the uncertainty in density (\bar{N}). Following these computations, mean rates of cohort-specific areal production were compared among creeks with one-way analysis of variance (ANOVA).

Relating production to environmental factors Numerous creek- and landscape-level habitat and anthropogenic factors were initially considered for relating to production. These factors included percent watershed imperviousness, percent marsh area in the high tide wetted area of each creek ('percent marsh instream'), percent intertidal-sub-tidal vegetated edge in the high tide wetted area, mean depth of the creek channel at bank-full level, and the percent of marsh-fringed (non-developed) shoreline downstream of the sampled creek area but within an approximate maximum home range (200 m) of adult *Fundulus heteroclitus* (Skinner et al. 2005). Percent watershed imperviousness was considered because it is believed to be an anthropogenic stressor shaping nekton communities in both freshwater creeks (Wang et al. 2001) and tidal creeks (Holland et al. 2004; Krebs et al. 2014; Rudershausen et al. 2016). Marsh percentages instream and fringing downstream of sampled areas were considered due to the importance of salt marsh as habitat for feeding and refuge among numerous nekton species, including *Fundulus heteroclitus* (Kneib 1997a). Percent linear edge was examined due to its importance for physical access to the marsh surface (Peterson and Turner 1994; Minello et al. 2003) and since the magnitude of production of salt marsh nekton is linked to the amount of edge (Kneib 2003; Roth et al. 2008). Channel water depth was considered

because it is a determinant of fish communities in tidal creeks along the U.S. South Atlantic coastal plain (Bretsch and Allen 2006; Allen et al. 2007; Rudershausen et al. 2016 (Chapters 2 and 3)).

In contrast to these metrics, which had a single value per study creek/watershed, values for visually estimated coverage of *Spartina alterniflora* and water depth from individual throw trap deployments were not considered in models fitted to cohort-specific production estimates; these metrics were previously considered in models of throw trap recovery efficiency.

Pearson correlation coefficients were calculated to determine pairs of spatial factors strongly correlated with each other ($r > |0.5|$). It was found that percent marsh instream was strongly correlated with: percent edge ($r = 0.609$), percent fringing marsh downstream ($r = 0.946$) and channel depth ($r = -0.833$). In contrast, percent marsh instream was not strongly correlated with percent watershed imperviousness ($r = -0.377$). Due to these collinear relationships, percent edge, percent marsh downstream, and channel depth were eliminated from further consideration for their influence on production while percent marsh instream and percent watershed imperviousness were retained for model fitting to areal estimates of production on the marsh surface.

Non-spatial variables were also considered for their effects on production. Mean TL of each cohort at the start of each inter-monthly time interval was considered given the potential for production to vary, either due to changing densities or changing growth rates, among size classes of *Fundulus heteroclitus* (Hagan et al. 2007). Month at the onset of each time interval and year were considered as temporal factors. Mean creek-specific water

temperature (°C), which was autonomously logged in study creeks, was considered given the ability of temperature to affect rates of secondary production (Valiela 1984).

Normally distributed general linear models (GLMs) were fitted via Bayesian inference (Kéry 2010) to examine the relationship between mean cohort-specific production estimates and the aforementioned spatial, temporal, physical, and biological factors. Plots relating values of mean production to each of these factors incorporated into models revealed no indication of non-linearity. An uninformative normal prior probability distribution was assigned to the intercept (*alpha*) term (mean and precision of 0 and $1 * 10^{-6}$, respectively) as well as each partial regression coefficient (*beta*) in a model.

We initially considered a full model that contained all potential explanatory factors. Subsequent models were run without factors whose partial regression coefficients (2.5/97.5 credible intervals) broadly overlapped with zero. Each model was fitted by calling *JAGS* version 4.0 (Plummer 2015) through *R* (R Development Core Team 2011) and using the software interface package *R2jags* (Su and Yajima 2015). Each model was run using three chains of initial values and updated 10,000 times. Every 10th observation was retained to reduce autocorrelation between successive updates. The initial 10% of retained updates of each parameter were discarded as a burn-in phase. Convergence was assessed by computing the Gelman-Rubin statistic for each model parameter; values less than 1.1 for this statistic suggest convergence to a stable posterior probability distribution (Gelman et al. 1996). A Bayesian p-value, used to assess model goodness of fit (Kéry 2010), was calculated for each model run.

We used two criteria to assess the results of model fitting and the factors that each model contained. The first criteria was the values for the 2.5/97.5 credible intervals of partial

regression coefficients; factors whose credible intervals overlapped with zero were assumed to not be meaningful covariates of production. The second criteria was using Deviance Information Criteria (DIC); the model that has the lowest DIC value would be the best at predicting replicate data with the same structure as the data that was observed (Spiegelhalter et al. 2002). A difference in DIC values > 5 units between any two fitted models is considered substantial (Spiegelhalter et al. 2002). Weights (w_i) of each model were calculated using the formula, $w_i = \exp(-DIC/2)$ (Spiegelhalter et al. 2002). The proportional w_i of each model was then calculated by dividing each w_i by the sum of weights across all of the fitted models in each set.

Relating adult abundance to larval/juvenile production In earlier work (Chapter 5) we found that the relative abundance of adult *Fundulus heteroclitus* was positively related to the instream percentages of salt marsh across high tide wetted areas in tidal creeks. Because of the tight linkage between larval and juvenile *Fundulus heteroclitus* and emergent marsh vegetation (Kneib 1997), higher creek-wide production of young fish is one mechanism that may explain the relationship between greater adult abundance and more area of salt marsh within a creek. To examine greater creek-wide (whole-creek) production of larval/juvenile fish as a potential mechanism for greater adult abundances in some creeks than others, we tested the relationship between springtime (April-June) larval/juvenile production and subsequent minnow trap catch of recently recruited adult fish (in fall of the same year) to determine whether production of larval and juvenile fish (extrapolated to the entire high tide wetted area of creeks) explained higher creek-wide numbers of adult recruits.

Testing for a relationship between larval/juvenile production and catches of adults was done in several steps. Each mean cohort-specific estimate of areal production in the

marsh for the April-May and May-June time periods was extrapolated to the full high wetted area. This was done by multiplying each mean areal within-marsh areal production estimate by the proportion of each creek's high tide wetted area that was marsh habitat (Table 6.1). We felt justified in extrapolating production on the marsh surface to the full high tide wetted area of each creek for this exercise because production of larval and juvenile *Fundulus heteroclitus* appears to be relegated exclusively to the marsh surface (Kneib 1984; Talbot and Able 1984; Teo and Able 2003b). Length frequency histograms (Figure 6.3) suggested that these fish tracked for production in the spring (April – June) of each year were young-of-year individuals rather than fish that had been spawned the summer/autumn before. Extrapolated rates of mean production were then summed across all cohorts tracked between April and June of each year in each creek to account for the springtime production that could contribute to subsequent recruitment of adults later in the same year.

The data used for adult *Fundulus heteroclitus*, to examine the relationship between larval/juvenile production and subsequent adult recruitment, were the mean creek-wide catches of fish in September 2012 and September 2013, respectively, using baited Gee-style 6.4 mm mesh wire minnow traps passively fished over 3-hour soak times around high tides (catch-per-unit-effort (CPUE) data; Chapter 5). Based on growth rates of throw-trapped fish tracked for production (see *Results*) and low survival of adult fish, we felt that using CPUE data from September of each year would allow us to examine minnow trap catches of adult fish that were likely to contain a high proportion of age-0 fish spawned earlier in the same year (Kneib and Stiven 1978). Minnow trap CPUE over 3-hour soak times has been established as a proxy for creek-wide densities of adult fish in these systems (Chapter 5).

Finally, the relationship between extrapolated larval/juvenile production and adult CPUE was tested using the Pearson correlation coefficient.

RESULTS

Estimates of density, growth and production from throw trap collections Mean densities (S.D.) of *Fundulus heteroclitus* of across all months and both years were 4.51 (5.18), 5.00 (5.74), 2.50 (2.84), 2.60 (3.26), and 2.99 (2.98) individuals m⁻² for Atlantic Veneer, Porters, Pelletier East, Pelletier West and Spooners Creeks, respectively. Some individuals collected by the throw trap were not used to estimate production due to the inability to identify and track their cohorts. In general there was high variability about each mean value and wide overlap among creeks in the densities of individual cohorts tracked for production (Figure 6.4; Table 6.2).

Estimated cohort-specific absolute growth rates ranged from 0.08 to 0.72 mm day⁻¹ (Table 6.2). There was variation in absolute growth rates among creeks but overall the values were fairly consistent and averaged 0.34 mm day⁻¹ (S.D. 0.14 mm day⁻¹) (Figure 6.5; Table 6.2). There was not a consistent trend in changes in absolute growth rates as a function of initial mean size of a cohort or with the progression of the growing season each year (Figure 6.5; Table 6.2). Rates of instantaneous growth (G_{inst}) varied by creek, month and initial mean size in a similar fashion as described for absolute growth rates above (Table 6.2).

A total of 69 estimates of areal production within marsh habitats were made. Across all creeks and time intervals, this dry weight production within marsh habitats averaged 0.0039 g m⁻² day⁻¹ (S.D. 0.0038 g m⁻² day⁻¹). There was considerable overlap in the variability about estimates of production on the marsh surface (Figure 6.6; Table 6.3) and

mean production values were not significantly different among creeks (one way ANOVA; $F = 0.386$, $p = 0.537$, degrees of freedom = 67).

Relating production to environmental factors The model that received the most support (lowest DIC score) contained four factors: year, fish size (TL), percent marsh in the high tide wetted area of each creek (MARSH) and percent imperviousness in each creek's watershed (IMPERV). In this model the dry weight areal production within marsh habitats (P) was given by the equation,

$$P = -0.000079*Year + 0.00012*TL + 0.00001*MARSH + 0.00003*IMPERV$$

In this model the 2.5 and 97.5 credible intervals about fish size did not overlap with zero (Figure 6.7) while the credible intervals about year and percent watershed imperviousness did overlap with zero. Also in this model, the 2.5 credible interval for percent marsh was equal to zero.

Of the eight models fitted to production and environmental data, there were five models that received support and were within 5 DIC units of the best fitting model (Table 6.4). Across all models receiving support, fish size and year were positive covariates of areal production but year, month, water temperature and percent watershed imperviousness were not related to production. The 2.5 credible interval for percent marsh instream was zero for all models but the median and 97.5 credible intervals for this factor were positive for all models. Parameters for each model adequately converged to stable posterior distributions and goodness of fit tests revealed an adequate fit of each model to the data.

Relating adult abundance to larval/juvenile production The relationship between adult CPUE in September of each year and cumulative April-June production extrapolated to the full high

tide wetted area of each creek was positive (Pearson $r = 0.627$) (Figure 6.8). It had a marginally significant p-value ($p = 0.052$).

DISCUSSION

Estimates of production and relationship with factors tested in GLMs We estimated production of larval/juvenile *Fundulus heteroclitus* in multiple tidal creeks and related these estimates to a number of potentially meaningful factors. Fitting general linear models to areal production estimates within salt marsh habitats revealed that the percentage of salt marsh in each creek and watershed imperviousness were not related to areal production within salt marsh habitats; while these two factors were in the best-fitting model (lowest DIC score), the 2.5 and 97.5 credible intervals either were zero (percent marsh) or overlapped with zero (percent watershed imperviousness) in this model and other models that were fitted. The results demonstrate the capacity for *Fundulus heteroclitus* to maintain larval/juvenile production on an area-by-area basis within marsh habitats even in creek watersheds with high percentages of developed land surface. Even a study creek that had lost a large amount of marsh area due to development (Pelletier East: Table 6.1) still retained linear marsh/creek edge found to be important for secondary production in marsh systems (Kneib 2003). This offers an explanation as to why this creek maintained rates of areal production in salt marsh relative to the other study creeks that had lesser instream impacts. The significant year effect in GLMs is symptomatic of the temporal variability that can be expected in estimating rates such as production in dynamic estuarine habitats (Able 1999).

Relating adult Fundulus heteroclitus abundance to larval/juvenile production Valiela et al. (1977) speculated that the catch of larval/juvenile *Fundulus heteroclitus* could be used as a recruitment index for adult fish. A relationship between larval/juvenile production at the

creek level and an index of adult abundance would be expected in these systems given similar rates of summertime apparent survival among creeks as well as seemingly minimal recruitment of fish from areas outside of each creek (Chapter 5). The observed positive relationship between cumulative larval/juvenile springtime production (extrapolated to the full high tide wetted area in each creek) and adult abundance later the same year (September) suggests that higher amounts of absolute production of larval and juvenile fish across the full high tide area in each creek is a likely mechanism explaining higher numbers of adults in some creeks than others. Thus, the obligate use of vegetated marsh by larval/juvenile *Fundulus heteroclitus* and the link between their production and adult abundance likely explains the relationship between adult density and the percentage of vegetated marsh creeks (Chapter 5). These estimates of larval/juvenile production extrapolated to full high tide areas can be useful for comparing the ability of creeks to ‘trophically relay’ nekton production to open-water estuaries (Kneib 2000). It is clear from this study that the trophic support provided by this keystone species (creek-wide production of this species that is available for export) is greater in creeks possessing more intact marsh mosaics.

Comparing production estimates to other studies A chief aim of this study was to relate *Fundulus heteroclitus* production to habitat and anthropogenic effects. We sampled in the same months and years across a habitat gradient in our study creeks and applied a consistent method to estimate production across study systems so that we could identify important covariates of production. Caution is advised when attempting to compare these estimates of cohort-specific larval/juvenile *Fundulus heteroclitus* production to other studies. In this study not all throw trapped individuals could be assigned to cohorts and thus not all of them were used to estimate production between successive monthly sampling events.

Additionally, some studies of *Fundulus heteroclitus* production have been conducted over seasons (fall-winter) (e.g., Teo and Able 2003a) when data were not collected for this study.

Hagan et al. (2007) may have dry weight production estimates most comparable to this study because they were collected over the summer growing season, in similar marsh habitats, and over similar sizes of *Fundulus heteroclitus*. In that study mean estimates of areal production within marsh habitats (converting monthly instantaneous growth rates to daily rates for small fish (< 30 mm standard length)) were 0.024, 0.059, and 0.090 g m⁻² day⁻¹ for three inter-monthly time periods during the summer. These estimates are higher than values in our study even when mean production estimates (Table 6.3) are summed across cohorts and for those creeks/ inter-monthly periods where all collected larval/juvenile fish could be used for production estimates (because they could all be assigned to cohorts) (Figure 6.3). Our mean (across all creeks) production estimate under these conditions was 0.0023 g m⁻² day⁻¹ (S.D. 0.0016) (n = 17).

Density appears to vary widely in studies of small *Fundulus heteroclitus* and offers a likely explanation for differences in production between this study and others. For example, the mean density of larval and juvenile *Fundulus heteroclitus* was estimated to be 7.2 individuals m⁻² on a Georgia marsh surface but that estimate relied on a passive sampling gear and included data across all cohorts of individuals (Kneib 1997b). Two studies using a throw trap in a New Jersey *Spartina alterniflora* marsh estimated densities of 15.1 individuals m⁻² (Teo and Able 2003a) and 20.2 individuals m⁻² (Hagan et al. 2007). These densities are higher than the highest mean creek-specific density in this study (5 individuals m⁻²: Chapter 2). It is unknown why densities of age-0 *Fundulus heteroclitus* are roughly

two-and four-fold higher in New Jersey compared to the Georgia estimate (Kneib 1997b) and our highest estimate in this study.

The method used in this study to estimate absolute density of age-0 *Fundulus heteroclitus* addresses a bias in failing to collect the full number of fish that are enclosed by the throw trap (recovery efficiency). However, it does not address potential capture inefficiency (Rozas and Minello 1997), which is avoidance of the gear by fish that the researcher is attempting to enclose. Deploying a throw trap around low tide, as done in the aforementioned New Jersey studies, would tend to minimize chances of escapement of fish from the sampling area (due to shallow depths). Thus, if capture efficiency is an issue in using a throw trap to collect age-0 *Fundulus heteroclitus*, it is likely more of an issue around high tides (such as in this study) where the chances of escapement of fish before trap deployment are theoretically higher. Sampling around high tide was done in this study to obtain an accurate representation of fish density over the full salt marsh area of each creek. The method of trap deployment in this study (afoot) would likely result in lower capture efficiency, if it is an issue, than deploying the trap from a boat or a raised platform (e.g., Teo and Able 2003a).

Growth rate appears to be less of an issue than density in contributing to discrepancies in production estimates between this study and others since rates are similar between this study and previous work on production of small *Fundulus heteroclitus*. The mean rate of absolute growth in this study (0.34 mm d^{-1} across all creeks) was similar to two New Jersey studies that have estimated absolute growth rates of juvenile *Fundulus heteroclitus* (Rountree 1992; Teo and Able 2003a; Hagan et al. 2007). Teo and Able (2003a) reported a range of absolute growth rates of small *Fundulus heteroclitus* ($< 30 \text{ mm}$

standard length) between roughly 0.23 and 0.30 mm d⁻¹ while Rountree (1992) and Hagan et al. (2007) respectively reported absolute growth of age-0 *Fundulus heteroclitus* to average 0.26 mm d⁻¹ (S.E. 0.02 mm d⁻¹) and 0.17 mm d⁻¹ in *Spartina alterniflora* habitats. The mean instantaneous growth rate across all creeks and time intervals in this study, when converted to a monthly time step (1.73 ± 1.14 (S.D.)), was roughly two-fold higher than those found by Hagan et al. (2007) for age-0 fish from a New Jersey *Spartina alterniflora* marsh but within the range (1.06 – 2.26) that Teo and Able (2003a) found for this age class from *Spartina alterniflora* habitats.

Potential sources of error Production, like other demographic rates, is a difficult metric to accurately measure due to the variability about estimates of fish abundance. This variability makes the detection of anthropogenic impacts difficult (Jones 1982). Further, estimates of secondary production are prone to error (Valiela 1984). Error in this study could have arisen from the mis-classification of individuals to their correct cohorts, extrapolating densities to areas over which throw trap sampling did not occur, and sampling over different days among study creeks within each lunar cycle. Some of these sources of error are discussed below.

This subjectivity in assigning membership of individual fish to cohorts could have biased growth rates. We evaluated the influence of biased growth rates on production relative to the influence of variable densities on production. This was done in several steps. First we introduced uncertainty in estimating absolute growth by both reducing and increasing rates of absolute growth by 20 percent for each of the 69 cohorts/time periods. Second, components of production (G_{inst} and \bar{B}) as well as production itself were recalculated using these intentionally biased-low and biased-high values of growth. For these calculations densities were held at their mean values in order to capture (isolate) the uncertainty in

growth. Third, for each of the 69 cohorts/time periods the percent increase between the biased-high- and biased-low production rates was calculated and then averaged across all 69 values. Finally, this mean was compared to the mean percent increase between the 2.5 and 97.5 CIs of production that used the variability about density when growth rate was fixed (see *Methods*). The variability about production due to variability in density was 28 times greater than due to the variability in growth. This is a minimum estimate of the magnitude of difference in production due to variability about density compared to growth because some 2.5 CI production estimates when variability about density was used were zero (cannot divide by zero). While the 20% bias rate in growth was arbitrarily chosen, this exercise supports the assertion that variability about production of this species is mainly due to variability about density rather than variability about growth (Teo and Able 2003). Thus, biases in growth rates based on mis-identifying cohort membership using length frequency histograms are likely to have relatively minor impact on estimates of production.

The degree to which the researcher can identify and distinguish cohorts in a distribution depends on how well modes are defined in length frequency plots. For several sampling periods and creeks, a larger sample size may have improved identification of these modes. Thus, a greater number of throw trap samples each month or more individuals per trap sample may have enabled us to better distinguish cohorts and assign group membership to more of the fish that were captured. However, with such regular (semi-monthly) spawning by this species (Taylor et al. 1979), the possibility exists that some cohorts would still be difficult to distinguish even with more individuals collected.

Mostly in later months sampling in each year, not all individual larval/juvenile *Fundulus heteroclitus* could be assigned to cohorts in this study. Thus, not all of them were

used to estimate production between successive monthly sampling events. Since production was estimated for individually identified cohorts and not across all individuals collected in each month/creek, this affected comparisons among creeks. However, we did sample across two years and seven months in creeks; such simultaneous sampling across all study systems increases the likelihood that any differences in monthly production among creeks, if they existed, would be detected.

Production assumes that the mean size of a cohort changes over time. Changes in the average length of a species over the time interval between samples may not be due to changes in length of individuals found within a study area but rather may occur from individuals recruiting from outside of study creeks (Bozeman Jr. and Dean 1980). In our case, we estimated production of larval/juvenile *Fundulus heteroclitus*, which are largely relegated to the marsh surface even over low tides (Kneib 1984; Talbot and Able 1984; Teo and Able 2003b). The residency of these young fish to the marsh platform decreases the likelihood that sampled individuals were recruits from outside of the five study areas where we sampled.

Changes in the average length of a species over the time interval between samples may also be due to size-selective mortality (Sogard 1997). Analyses into changes in the size distribution of a cohort over time, such as in this study, may confound changes in size distributions due to body size vs. changes due to mortality (Munch et al. 2003). Thus, our comparisons among salt marsh systems assume that this bias is consistent across marshes or does not occur.

Different sizes of fish among creeks, due to sampling them at different periods in the lunar cycle one or more months after a cohort was spawned, may have contributed to

differences in densities among creeks if capture efficiencies were less than 100% for larger, more mobile fish. The different times of sampling among creeks within a month may have contributed to different values of production, given that production was positively related to fish size.

For logistical reasons the throw trap could not be deployed in non-vegetated habitats. Salt marsh production should ideally be estimated for the full high tide wetted area since this is the area over which trophic support is provided for nekton populations inhabiting tidal creeks (Kneib 2003). However, small *Fundulus heteroclitus* targeted by the throw trap are found almost exclusively on the marsh surface (Kneib 1984; Kneib 1987; Kneib 1997b). Thus, it can be assumed that the density of larval/juvenile *Fundulus heteroclitus* was zero in non-vegetated sub-tidal areas of each creek.

The percentage of visually estimated marsh within each trap deployment likely did not influence the density of *Fundulus heteroclitus*. While some creeks had higher mean values of percent visually estimated *Spartina alterniflora* than others (Table 6.1), there was only a 20% difference between the creek with the lowest and greatest mean estimated value. Furthermore, mean throw trap density (across all cohorts) and mean percent estimated vegetated cover for each creek were not correlated ($r = -0.836$; $p = 0.078$). The bulk of the catch by the throw trap was age-0 fish and this age class uses both vegetated and non-vegetated meso-habitats within the marsh surface (Kneib 1984; Talbot and Able 1984). Thus, the estimated vegetative coverage within each trap deployment is unlikely to explain differences in densities and production estimates among creeks.

Conclusions We reject the hypothesis that watershed development categorically and negatively affects areal production of estuarine fishes (Jensen et al. 2014). Results from

model fitting to production estimates of larval/juvenile *Fundulus heteroclitus* should be useful to the North Carolina Division of Coastal Management, the natural resource agency tasked with planning and permitting development in the state's coastal zone. It is believed that watershed imperviousness is a composite measure of impacts to tidal creeks in the U.S. South Atlantic coastal zone, with irreversible changes occurring to biota when imperviousness exceeds roughly 30% (Holland et al. 2004). This may be true for a variety of mobile and sessile species (Holland et al. 2004; Krebs et al. 2014). However, results from this study suggest that areal production of the dominant nekton species in salt marsh habitats in Atlantic coastal tidal creeks is not negatively affected by watershed development as long as critical salt marsh habitat is not removed from intertidal areas. While areal rates of production within salt marsh habitats did not differ among creeks with different creek-wide percentages of salt marsh, creeks with a lower percentage of this habitat will have lower cumulative creek-wide production, translating into lower creek-wide densities of adults and lower amounts of trophic export (Kneib 2000).

Potential sources of error notwithstanding, results from this study emphasize that creek-wide decreases in the percentage of salt marsh and correlated development pressures (e.g., increasing in water depths) compared to baseline conditions will negatively affect creek-wide rates of *Fundulus heteroclitus* production. It is forecasted that anthropogenic activities in tidal creek watersheds and intertidal zones will further eliminate salt marsh habitats along United States coastlines (Kennish 2001; Mattheus et al. 2010; Gittman et al. 2015). These stressors increase the importance of maintaining and restoring salt marsh coverage to maintain creek-wide rates of secondary production of important nekton species that reflect rates in undisturbed systems.

Dahlgren et al. (2006) developed the concept of effective juvenile habitat to refer to estuarine habitats that make a greater-than-average contribution to adult populations. The authors believed that this concept facilitates the identification of habitats for conservation and restoration. This study identifies the areal value of salt marsh for larval/juvenile *Fundulus heteroclitus* production across creeks with a range of landscape-level impacts. The ability of this species to maintain areal rates of within-marsh production in otherwise impacted creeks should provide guidance to managers charged with protecting salt marsh patches threatened by development.

The serial replacement of intertidal salt marsh with hardened shoreline caps the amount of production that can be expected from any salt marsh (Lowe and Peterson 2014). The results from this study provide guidance to coastal planners that might otherwise deem salt marshes less worthy of protection if they have not been designated as strategic habitat areas or if their watersheds are viewed as being too developed to allow production and trophic relay to higher-level consumers in open-water estuaries (Kneib 2000).

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Table 6.1. Watershed, habitat and water quality characteristics for five tidal creeks in coastal North Carolina sampled for larval/juvenile *Fundulus heteroclitus* production from April through October of 2012 and 2013.

Characteristic / Measurement	Atlantic Veneer	Porters	Pelletier East	Pelletier West	Spooners
Watershed area (m ²)	414,224	1,095,729	1,127,387	698,413	490,859
Impervious area (m ²)	64,322	110,166	260,740	325,629	64,220
Inter-tidal-sub-tidal vegetated edge (m)	500	1200	145	500	400
Percent watershed imperviousness	15.5	10.0	23.1	46.7	13.0
High tide wetted area (m ²)	5,209	15,162	4,170	5,427	7,691
Marsh area (m ²)	4,247	9,498	112	3,707	6,324
Percent marsh area instream at high tide	81.5	62.6	2.7	68.3	82.2
Percent marsh area downstream at high tide	91.0	100	0	34.5	37.3
Mean creek channel depth (m)	0.21	0.27	0.96	0.28	0.29
Mean sampling distance from channel (m), mean (SE)	5.8 (0.1)	11.25 (0.9)	0.4 (0.1)	4.7 (0.3)	3.5 (0.5)
Mean sampling depth (m), mean (SE)	0.19 (0.01)	0.24 (0.01)	0.19 (0.01)	0.19 (0.01)	0.19 (0.01)
Mean percent vegetative coverage (SE)	65.0 (1.6)	61.7 (1.7)	72.0 (2.4)	80.6 (1.6)	68.3 (1.8)
Mean temperature (°C), mean (SE)	24.9 (0.4)	26.0 (0.4)	27.6 (0.4)	26.8 (0.4)	27.3 (0.5)
Mean salinity (psu), mean (SE)	30.0 (0.7)	25.8 (0.5)	21.0 (0.9)	17.6 (0.8)	25.6 (1.0)
Mean dissolved oxygen (mg/l), mean (SE)	4.83 (0.12)	5.26 (0.20)	5.7 (0.3)	5.0 (0.27)	4.2 (0.2)

Table 6.2. Cohort-specific growth and density data used to estimate production of *Fundulus heteroclitus* sampled with a 1 m² throw trap from April through October of 2012 and 2013 in salt marshes of five tidal creeks in coastal North Carolina. Data include: span (days) between successive samples, mean estimated total length (TL, mm) and dry weight (DW, g), mean absolute growth in length (Growth, mm/day), mean estimated instantaneous growth (G_{inst} , day⁻¹), and the mean density (individuals m⁻²) (2.5/97.5 credible intervals in parenthesis) estimated for the first month (\bar{N}_1) and second month (\bar{N}_2) for each cohort and time interval tracked. Negative values for 2.5 CIs of \bar{N} were changed to zero. Different numbers of cohorts were tracked among creeks and time intervals. Growth in weight was estimated from creek-specific linear regressions relating dry weight to total length. Creek abbreviations: AV = Atlantic Veneer, P = Porters, PE = Pelletier East, PW = Pelletier West, S = Spooners.

Creek	Year	Months	Span	TL ₁	TL ₂	Growth	DW ₁	DW ₂	G_{inst}	\bar{N}_1	\bar{N}_2
AV	2012	Apr-May	27	10.1	21.9	0.44	0.0061	0.0333	0.0629	0.60 (0 - 1.26)	0.70 (0 - 1.53)
		May-Jun	36	10.1	23.0	0.36	0.0061	0.0370	0.0501	1.10 (0.16 - 2.04)	1.20 (0.24 - 2.16)
		May-Jun	36	21.9	41.4	0.54	0.0333	0.1426	0.0404	0.70 (0 - 1.53)	0.80 (0 - 2.16)
		Jun-Jul	27	10.6	20.6	0.37	0.0063	0.0306	0.0585	1.40 (0.12 - 2.68)	1.30 (0.36 - 2.24)
		Jun-Jul	27	23.0	36.1	0.49	0.0370	0.1021	0.0376	1.20 (0.24 - 2.16)	0.20 (0 - 0.59)
		Jul-Aug	35	7.1	14.1	0.20	0.0025	0.0125	0.0460	0.40 (0 - 0.83)	0.80 (0.16 - 1.44)
		Jul-Aug	35	20.6	30.2	0.27	0.0306	0.0693	0.0234	1.30 (0.32 - 2.27)	2.30 (1.13 - 3.47)
		Aug-Sep	32	14.1	30.1	0.50	0.0135	0.0944	0.0608	0.80 (0.16 - 1.44)	1.40 (0.42 - 2.38)
		Aug-Sep	32	30.2	41.4	0.35	0.0977	0.2250	0.0261	2.30 (1.13 - 3.47)	1.50 (0.66 - 2.34)
	Sep-Oct	30	30.1	44.5	0.48	0.0944	0.2727	0.0354	1.40 (0.42 - 2.38)	1.30 (0.13 - 2.47)	
	2013	Apr-May	27	6.6	16.6	0.37	0.0020	0.0170	0.0793	0.70 (0 - 1.42)	0.80 (0 - 1.72)
		May-Jun	27	6.6	16.1	0.35	0.0020	0.0156	0.0761	4.20 (1.94 - 6.46)	1.30 (0 - 2.81)
		May-Jun	27	16.6	23.8	0.27	0.0170	0.0389	0.0307	0.80 (0 - 1.72)	0.40 (0 - 1.00)
		Jun-Jul	21	7.7	14.3	0.31	0.0032	0.0122	0.0637	2.90 (0.42 - 4.38)	1.50 (0.71 - 2.29)
		Jul-Aug	25	14.3	27.5	0.53	0.0122	0.0565	0.0613	1.50 (0.71 - 2.29)	0.70 (0 - 1.47)
Aug-Sep		34	6.7	17.4	0.31	0.0019	0.0211	0.0708	0.60 (0.17 - 1.03)	2.30 (0.73 - 3.87)	
P	2012	Sep-Oct	33	17.4	24.0	0.20	0.0211	0.0530	0.0279	2.30 (0.73 - 3.87)	1.40 (0.51 - 2.29)
		Apr-May	24	11.8	13.9	0.09	0.0047	0.0055	0.0065	0.40 (0 - 1.00)	4.00 (0.22 - 7.77)
		May-Jun	31	13.9	17.4	0.11	0.0055	0.0154	0.0332	4.00 (0.22 - 7.77)	2.50 (0.86 - 4.14)
		Jun-Jul	33	17.4	20.7	0.10	0.0154	0.0306	0.0208	2.50 (0.86 - 4.14)	5.50 (0.89 - 10.11)
		Jul-Aug	31	20.7	29.4	0.28	0.0306	0.0971	0.0372	5.50 (0.89 - 10.11)	3.30 (1.17 - 5.43)
		Aug-Sep	36	9.7	19.3	0.27	0.0019	0.0200	0.0654	1.90 (0.49 - 3.31)	2.10 (0.57 - 3.63)
		Aug-Sep	36	18.5	33.3	0.41	0.0167	0.1161	0.0539	2.50 (0.43 - 4.57)	1.50 (0.71 - 2.29)
		Sep-Oct	22	19.3	25.6	0.29	0.0200	0.0517	0.0432	2.10 (0.57 - 3.63)	2.90 (0.52 - 5.28)
		Sep-Oct	22	33.3	38.8	0.25	0.1161	0.1928	0.0231	1.50 (0.71 - 2.29)	0.90 (0.10 - 1.70)
	2013	Apr-May	33	7.1	20.4	0.40	0.0004	0.0234	0.1233	0.30 (0 - 0.89)	1.00 (0.49 - 1.51)

		May-Jun	25	10.6	18.8	0.41	0.0021	0.0180	0.0859	2.80 (0.38 - 5.22)	1.90 (0.65 - 3.15)
		May-Jun	25	20.4	29.4	0.36	0.0234	0.0942	0.0557	1.00 (0.49 - 1.51)	0.80 (0 - 1.80)
		Jun-Jul	24	9.4	17.0	0.32	0.0012	0.0126	0.0980	1.10 (0.42 - 1.78)	0.40 (0 - 0.83)
		Jun-Jul	24	18.8	29.2	0.43	0.0180	0.0946	0.0691	1.90 (0.65 - 3.15)	0.50 (0.06 - 0.94)
		Jul-Aug	18	6.6	12.9	0.35	0.0003	0.0040	0.1439	1.00 (0.22 - 1.77)	0.40 (0 - 0.83)
		Jul-Aug	18	17.0	19.2	0.12	0.0126	0.0194	0.0240	0.40 (0 - 0.83)	1.60 (0.87 - 2.33)
		Jul-Aug	18	29.2	30.7	0.08	0.0946	0.1109	0.0088	0.50 (0.06 - 0.94)	0.90 (0 - 1.93)
		Aug-Sep	38	12.9	17.8	0.13	0.0049	0.0144	0.0284	0.40 (0 - 0.83)	2.60 (0.95 - 4.25)
		Aug-Sep	38	19.2	27.2	0.21	0.0192	0.0600	0.0300	1.60 (0.87 - 2.33)	1.80 (0.64 - 2.96)
		Aug-Sep	38	30.7	39.6	0.23	0.0877	0.2046	0.0223	0.90 (0 - 1.93)	0.40 (0.08 - 0.72)
		Sep-Oct	29	9.1	20.7	0.40	0.0017	0.0243	0.0917	1.60 (0.54 - 2.66)	2.30 (1.02 - 3.58)
		Sep-Oct	29	17.8	29.8	0.41	0.0144	0.0802	0.0592	2.60 (0.84 - 4.25)	2.80 (1.03 - 4.57)
		Sep-Oct	29	27.2	39.6	0.43	0.0600	0.2026	0.0420	1.80 (0.65 - 2.96)	0.30 (0 - 0.60)
PE	2012	May-Jun	34	7.0	19.3	0.36	0.0013	0.0158	0.0735	0.40 (0.15 - 1.85)	0.55 (0 - 0.88)
		Jun-Jul	30	10.3	23.1	0.43	0.0043	0.0268	0.0610	2.80 (0.53 - 5.07)	1.00 (0 - 2.34)
		Jul-Aug	29	10.6	18.5	0.27	0.0036	0.0151	0.0494	0.83 (0 - 1.77)	2.00 (0 - 4.14)
		Jul-Aug	29	23.1	30.0	0.24	0.0268	0.0510	0.0222	1.00 (0 - 2.34)	1.43 (0.70 - 2.16)
		Aug-Sep	39	8.1	16.4	0.21	0.0013	0.0128	0.0586	1.57 (0 - 3.38)	1.00 (0 - 2.04)
		Aug-Sep	39	18.5	27.4	0.23	0.0175	0.0548	0.0293	2.00 (0 - 4.14)	1.14 (0.35 - 1.93)
		Aug-Sep	39	30.0	42.4	0.32	0.0733	0.2034	0.0262	1.43 (0.70 - 2.16)	0.71 (0 - 1.53)
		Sep-Oct	26	16.4	24.6	0.32	0.0128	0.0389	0.0428	1.00 (0 - 2.04)	0.43 (0 - 1.27)
	2013	May-Jun	20	7.1	16.6	0.48	0.0012	0.0110	0.1108	1.00 (0 - 2.38)	2.40 (0 - 5.35)
		Jun-Jul	32	9.1	13.2	0.13	0.0023	0.006	0.0300	0.40 (0 - 0.88)	0.33 (0 - 0.75)
		Jul-Aug	19	13.2	18.6	0.28	0.0060	0.0154	0.0496	0.33 (0 - 0.75)	0.40 (0 - 0.88)
		Aug-Sep	29	7.5	23.9	0.57	0.0011	0.0364	0.1207	1.00 (0 - 2.96)	0.67 (0.01 - 1.33)
PW	2012	May-Jun	23	6.5	23.0	0.72	0.0005	0.0548	0.2042	0.30 (0 - 0.72)	0.70 (0 - 1.47)
		Jun-Jul	32	6.5	23.3	0.53	0.0004	0.0604	0.1568	0.70 (0.34 - 1.05)	1.00 (0 - 2.17)
		Jul-Aug	28	23.3	34.2	0.39	0.0604	0.2313	0.0480	1.00 (0 - 2.17)	1.50 (0.52 - 2.48)
		Aug-Sep	38	8.9	20.9	0.32	0.0020	0.0332	0.0739	0.50 (0 - 0.94)	0.70 (0.04 - 1.36)
		Aug-Sep	38	23.0	30.0	0.18	0.0488	0.1000	0.0189	0.90 (0.10 - 1.70)	0.40 (0.08 - 0.72)
	2013	May-Jun	23	9.7	25.3	0.68	0.0032	0.0758	0.1376	0.80 (0 - 1.72)	0.60 (0.17 - 1.03)
		Aug-Sep	38	5.8	20.7	0.39	0.0005	0.0311	0.1087	1.30 (0.58 - 2.02)	1.10 (0.25 - 1.95)
		Sep-Oct	31	7.5	21.1	0.44	0.0012	0.0316	0.1055	0.50 (0 - 1.17)	0.20 (0 - 0.46)
		Sep-Oct	31	20.7	31.5	0.35	0.0311	0.1194	0.0434	1.10 (0.25 - 1.95)	0.60 (0.17 - 1.03)
S	2012	May-Jun	28	7.0	16.6	0.34	0.0022	0.0171	0.0732	1.00 (0 - 2.20)	1.20 (0 - 2.74)
		Jun-Jul	40	16.6	25.4	0.22	0.0171	0.0477	0.0256	1.20 (0 - 2.74)	2.50 (0.98 - 4.02)
		Jul-Aug	30	25.4	34.8	0.31	0.0477	0.0990	0.0243	2.50 (0.98 - 4.02)	1.90 (0.61 - 3.19)
		Aug-Sep	33	14.5	21.2	0.20	0.0128	0.0322	0.0280	0.80 (0.07 - 1.53)	1.40 (0.26 - 2.54)
		Sep-Oct	20	21.2	27.7	0.33	0.0322	0.0663	0.0361	1.40 (0.26 - 2.54)	0.90 (0.05 - 1.75)

2013	May-Jun	15	10.4	18.6	0.55	0.0062	0.0233	0.0883	0.70 (0 - 1.87)	0.40 (0.08 - 0.72)
	Jun-Jul	23	18.6	32.1	0.59	0.0233	0.0803	0.0538	0.40 (0.08 - 0.72)	0.40 (0.08 - 0.72)
	Jul-Aug	25	32.1	40.2	0.32	0.0803	0.1347	0.0207	0.40 (0.08 - 0.72)	0.30 (0 - 0.60)
	Sep-Oct	34	18.7	27.4	0.26	0.0228	0.0643	0.0305	4.00 (2.00 - 6.00)	1.10 (0.03 - 2.17)

Table 6.3. Estimated biomass and production for cohorts of *Fundulus heteroclitus* sampled with a 1 m² throw trap from April through October of 2012 and 2013 in salt marshes of five tidal creeks in coastal North Carolina. Data include the 2.5 confidence interval (CI), mean (m), and 97.5 CI of dry weight (\bar{B} , g) across successive months as well as the 2.5 CI, mean, and 97.5 CI of cohort-specific areal dry weight production on the marsh surface (P , g m⁻² day⁻¹). Creek abbreviations: AV = Atlantic Veneer, P = Porters, PE = Pelletier East, PW = Pelletier West, S = Spooners.

Creek	Year	Months	$\bar{B}_{2.5}$	\bar{B}_m	$\bar{B}_{97.5}$	$P_{2.5}$	P_m	$P_{97.5}$	
AV	2012	Apr-May	0.0000	0.0135	0.0293	0.0000	0.0009	0.0018	
		May-Jun	0.0049	0.0256	0.0462	0.0003	0.0013	0.0023	
		May-Jun	0.0000	0.0687	0.1795	0.0000	0.0028	0.0073	
		Jun-Jul	0.0059	0.0243	0.0427	0.0003	0.0014	0.0025	
		Jun-Jul	0.0044	0.0324	0.0701	0.0002	0.0012	0.0026	
		Jul-Aug	0.0010	0.0055	0.0100	0.0001	0.0003	0.0005	
		Jul-Aug	0.0441	0.0996	0.1550	0.0010	0.0023	0.0036	
		Aug-Sep	0.0209	0.0715	0.1221	0.0013	0.0043	0.0074	
		Aug-Sep	0.1295	0.2811	0.4328	0.0034	0.0073	0.0113	
		Sep-Oct	0.0375	0.2433	0.4491	0.0013	0.0086	0.0159	
		2013	Apr-May	0.0000	0.0075	0.0160	0.0000	0.0006	0.0013
			May-Jun	0.0019	0.0143	0.0284	0.0002	0.0011	0.0022
			May-Jun	0.0000	0.0146	0.0341	0.0000	0.0005	0.0010
			Jun-Jul	0.0050	0.0138	0.0210	0.0003	0.0009	0.0013
Jul-Aug	0.0043		0.0289	0.0555	0.0003	0.0018	0.0034		
Aug-Sep	0.0079		0.0248	0.0418	0.0006	0.0018	0.0030		
Sep-Oct	0.0212		0.0614	0.1015	0.0006	0.0017	0.0028		
P	2012	Apr-May	0.0006	0.0119	0.0237	0.0000	0.0001	0.0002	
		May-Jun	0.0072	0.0303	0.0532	0.0002	0.0010	0.0018	
		Jun-Jul	0.0202	0.1034	0.1866	0.0004	0.0022	0.0039	
		Jul-Aug	0.0704	0.2444	0.4183	0.0026	0.0091	0.0156	
		Aug-Sep	0.0062	0.0228	0.0394	0.0004	0.0015	0.0026	
		Aug-Sep	0.0448	0.1080	0.1711	0.0024	0.0058	0.0092	
		Sep-Oct	0.0191	0.0960	0.1728	0.0008	0.0041	0.0075	
		Sep-Oct	0.0509	0.1738	0.2968	0.0012	0.0040	0.0068	

	2013	Apr-May	0.0057	0.0118	0.0178	0.0007	0.0015	0.0022
		May-Jun	0.0062	0.0200	0.0338	0.0005	0.0017	0.0029
		May-Jun	0.0057	0.0494	0.1024	0.0003	0.0028	0.0057
		Jun-Jul	0.0003	0.0032	0.0063	0.0000	0.0003	0.0006
		Jun-Jul	0.0087	0.0408	0.0728	0.0006	0.0028	0.0050
		Jul-Aug	0.0000	0.0010	0.0019	0.0000	0.0001	0.0003
		Jul-Aug	0.0084	0.0180	0.0278	0.0002	0.0004	0.0007
		Jul-Aug	0.0028	0.0736	0.1515	0.0000	0.0007	0.0013
		Aug-Sep	0.0068	0.0197	0.0326	0.0002	0.0006	0.0009
		Aug-Sep	0.0276	0.0694	0.1112	0.0008	0.0021	0.0033
		Aug-Sep	0.0082	0.0804	0.1583	0.0002	0.0018	0.0035
		Sep-Oct	0.0129	0.0293	0.0458	0.0012	0.0027	0.0042
		Sep-Oct	0.0474	0.1310	0.2139	0.0028	0.0078	0.0127
		Sep-Oct	0.0195	0.0844	0.1496	0.0008	0.0035	0.0063
PE	2012	May-Jun	0.0001	0.0046	0.0082	0.0000	0.0003	0.0006
		Jun-Jul	0.0011	0.0194	0.0423	0.0001	0.0012	0.0026
		Jul-Aug	0.0000	0.0166	0.0344	0.0000	0.0008	0.0017
		Jul-Aug	0.0179	0.0499	0.0864	0.0004	0.0011	0.0019
		Aug-Sep	0.0000	0.0074	0.0153	0.0000	0.0004	0.0009
		Aug-Sep	0.0096	0.0487	0.0891	0.0003	0.0014	0.0026
		Aug-Sep	0.0257	0.1246	0.2348	0.0007	0.0033	0.0061
		Sep-Oct	0.0000	0.0148	0.0378	0.0000	0.0006	0.0016
	2013	May-Jun	0.0000	0.0138	0.0309	0.0000	0.0015	0.0034
		Jun-Jul	0.0000	0.0015	0.0033	0.0000	0.0000	0.0001
		Jul-Aug	0.0000	0.0041	0.0090	0.0000	0.0002	0.0005
		Aug-Sep	0.0002	0.0127	0.0258	0.0000	0.0015	0.0031
PW	2012	May-Jun	0.0000	0.0193	0.0405	0.0000	0.0039	0.0083
		Jun-Jul	0.0001	0.0303	0.0657	0.0000	0.0048	0.0103
		Jul-Aug	0.0601	0.2037	0.3523	0.0029	0.0098	0.0169
		Aug-Sep	0.0007	0.0121	0.0235	0.0001	0.0009	0.0017
		Aug-Sep	0.0064	0.0420	0.0775	0.0001	0.0008	0.0015
	2013	May-Jun	0.0064	0.0240	0.0418	0.0009	0.0033	0.0058

		Aug-Sep	0.0040	0.0174	0.0308	0.0004	0.0019	0.0034
		Sep-Oct	0.0000	0.0035	0.0080	0.0000	0.0004	0.0008
		Sep-Oct	0.0140	0.0529	0.0918	0.0006	0.0023	0.0040
S	2012	May-Jun	0.0000	0.0114	0.0258	0.0000	0.0008	0.0019
		Jun-Jul	0.0234	0.0699	0.1193	0.0006	0.0018	0.0031
		Jul-Aug	0.0536	0.1537	0.2538	0.0013	0.0037	0.0062
		Aug-Sep	0.0046	0.0277	0.0507	0.0001	0.0008	0.0014
		Sep-Oct	0.0058	0.0524	0.0989	0.0002	0.0019	0.0036
	2013	May-Jun	0.0009	0.0068	0.0142	0.0001	0.0006	0.0013
		Jun-Jul	0.0041	0.0207	0.0373	0.0002	0.0011	0.0020
		Jul-Aug	0.0032	0.0363	0.0693	0.0001	0.0008	0.0014
		Sep-Oct	0.0238	0.0810	0.1382	0.0007	0.0025	0.0042

Table 6.4. Bayesian probability values (p), DIC values, and 2.5, median and 97.5 credible intervals of partial regression coefficients from fitting general linear models to mean areal estimates of dry weight production ($\text{g m}^{-2} \text{day}^{-1}$) of *Fundulus heteroclitus* on the vegetated marsh surface of five North Carolina tidal creeks in 2012-13. See *Methods* section for description of factors considered and model development. ΔDIC is the difference between the DIC value for the best fitting model (lowest DIC score) and each model fitted. Proportional model weight is w_i . Model #5 is the full model. ‘Null’ is the intercept-only model (Model #10).

Model #	Covariate	p	DIC	ΔDIC	w_i	2.5	Median	97.5
1	Year	0.511	-658.7	0	0.25	-0.00175	-0.00079	0.00019
	Total length					0.00005	0.00012	0.00018
	Percent marsh instream					0.00000	0.00001	0.00003
	Percent watershed imperviousness					-0.00001	0.00003	0.00007
2	Year	0.534	-658.1	0.6	0.19	-0.00180	-0.00091	0.00009
	Total length					0.00005	0.00011	0.00017
	Percent marsh instream					0.00000	0.00001	0.00003
3	Year	0.523	-658.1	0.6	0.19	-0.00177	-0.00080	0.00013
	Total length					0.00005	0.00011	0.00018
4	Year	0.539	-657.8	0.9	0.16	-0.00169	-0.00073	0.00026
	Total length					0.00006	0.00012	0.00019
	Percent watershed imperviousness					-0.00001	0.00003	0.00007
5	Total length	0.528	-657.7	1.0	0.15	0.00006	0.00012	0.00018
6	Year	0.516	-656.0	2.7	0.06	-0.00176	-0.00079	0.00018
	Month					-0.00019	0.00017	0.00054
	Water temperature					-0.00028	-0.00008	0.00011
	Total length					0.00003	0.00010	0.00017
	Percent marsh instream					0.00000	0.00001	0.00003
	Percent watershed imperviousness					-0.00001	0.00003	0.00008
7	Year	0.533	-648.2	10.5	0.00	-0.00213	-0.00108	-0.00003
8	Null	0.500	-645.9	12.8	0.00	-	-	-

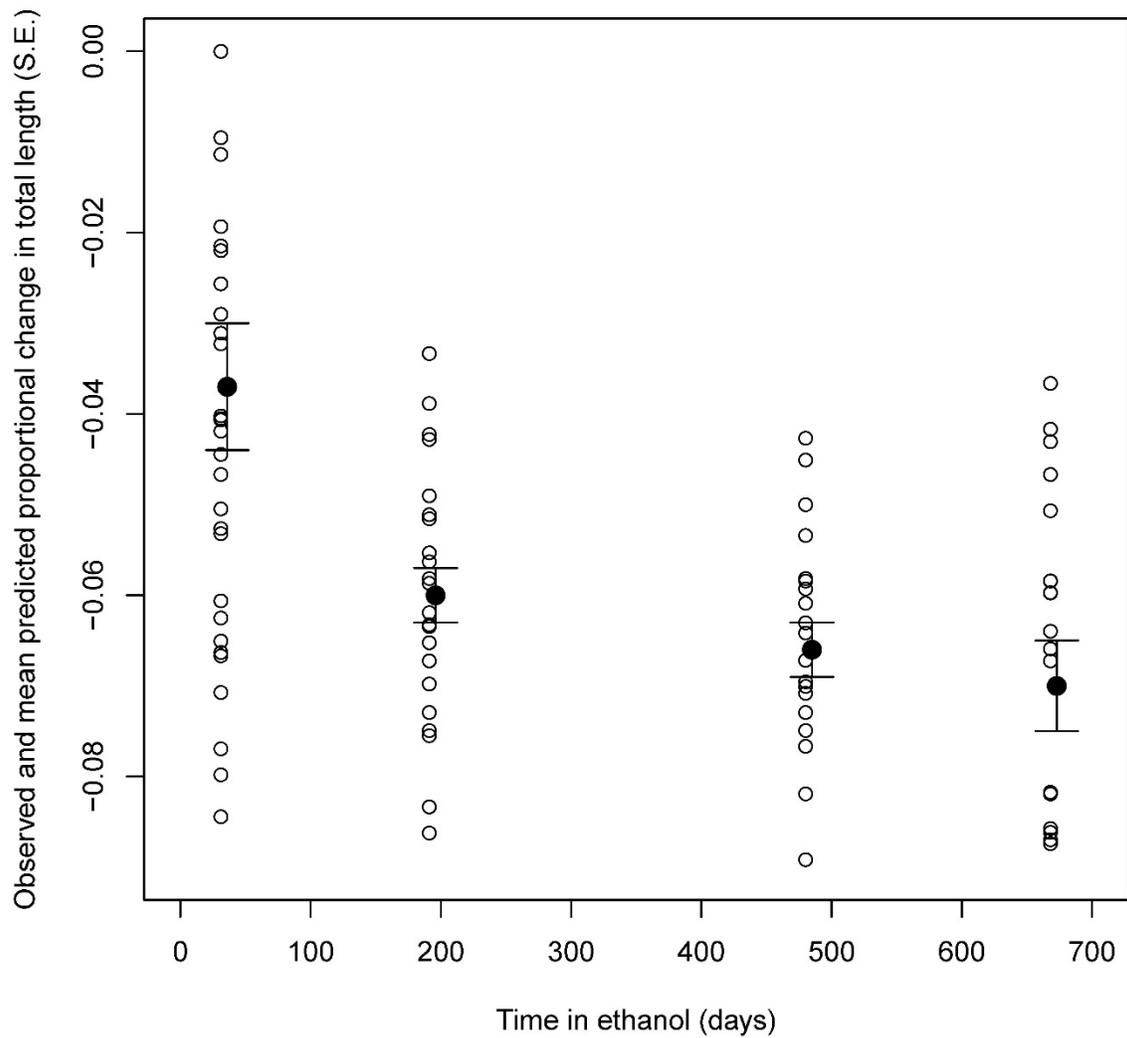


Figure 6.1. Relationship between observed (open symbols) and mean predicted proportional shrinkage (filled symbols) (\pm standard error (SE), lines) (y axis) vs. elapsed time after collection (days) (x axis) for *Fundulus heteroclitus* captured from five tidal creeks in coastal North Carolina and preserved in 95% denatured ethanol. Observed points are jittered around their true x-values to avoid overlap with the symbols that represent predicted values.

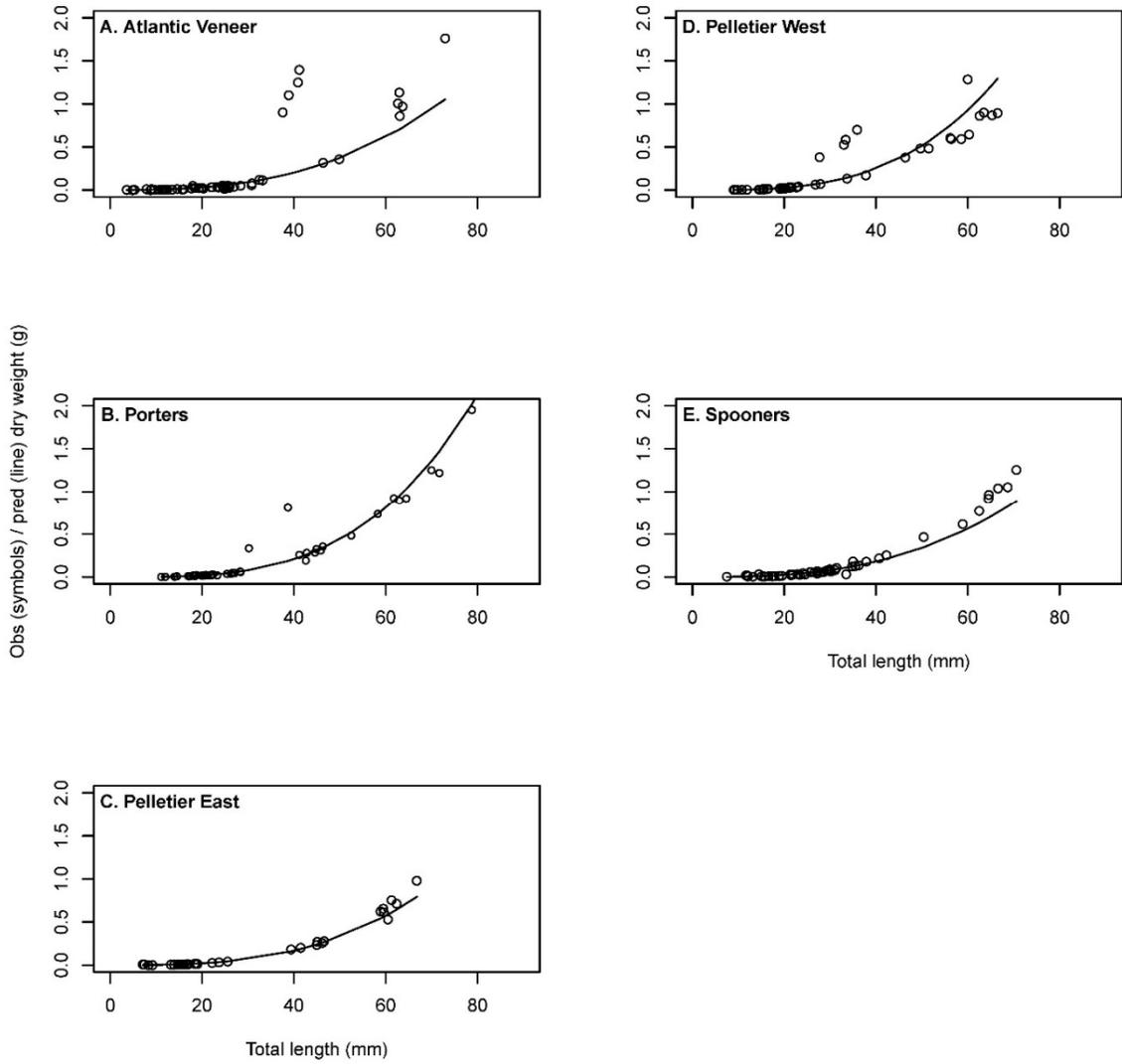


Figure 6.2. Non-linear relationships between dry weight [g: observed (‘obs’: open symbols) and predicted (‘pred’: line) (y axis)] and total length (mm) (x axis) for *Fundulus heteroclitus* captured from five tidal creeks in coastal North Carolina. The ranges of the x and y axes are identical among panels.

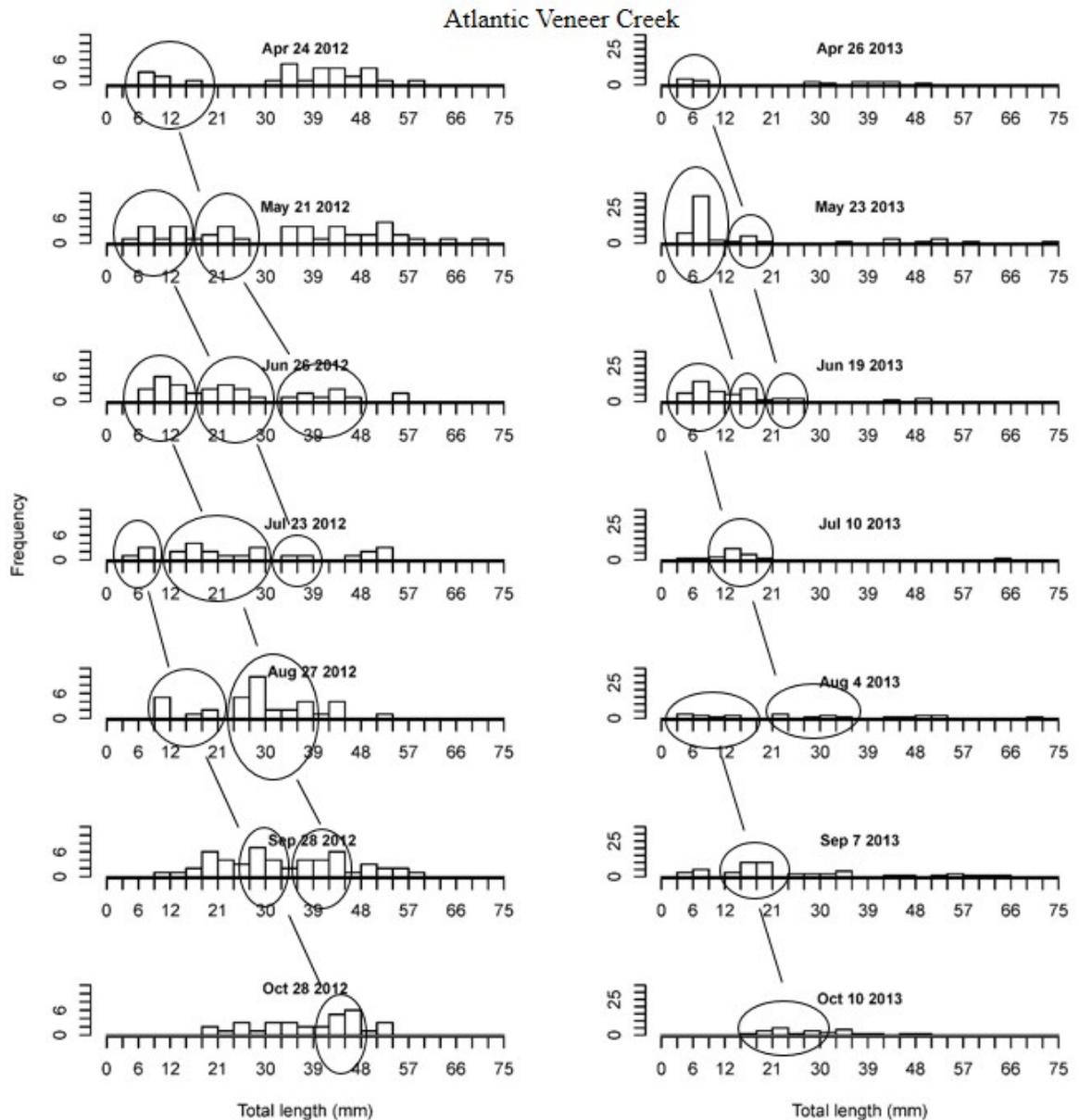


Figure 6.3. Numbers of *Fundulus heteroclitus* captured by deploying a 1 m² throw trap on the marsh surface (y axis) by total length (3 mm length bins) (x axis). Data were collected in five tidal creeks in coastal North Carolina from April through October 2012 and 2013. The x axes are identical among panels within- and among creeks. The y axes are identical among the five panels within each creek and year combination. Ellipses and lines show each cohort tracked from one month to the next to calculate cohort-specific growth rates. The number of cohorts that were tracked differed among creeks and months.

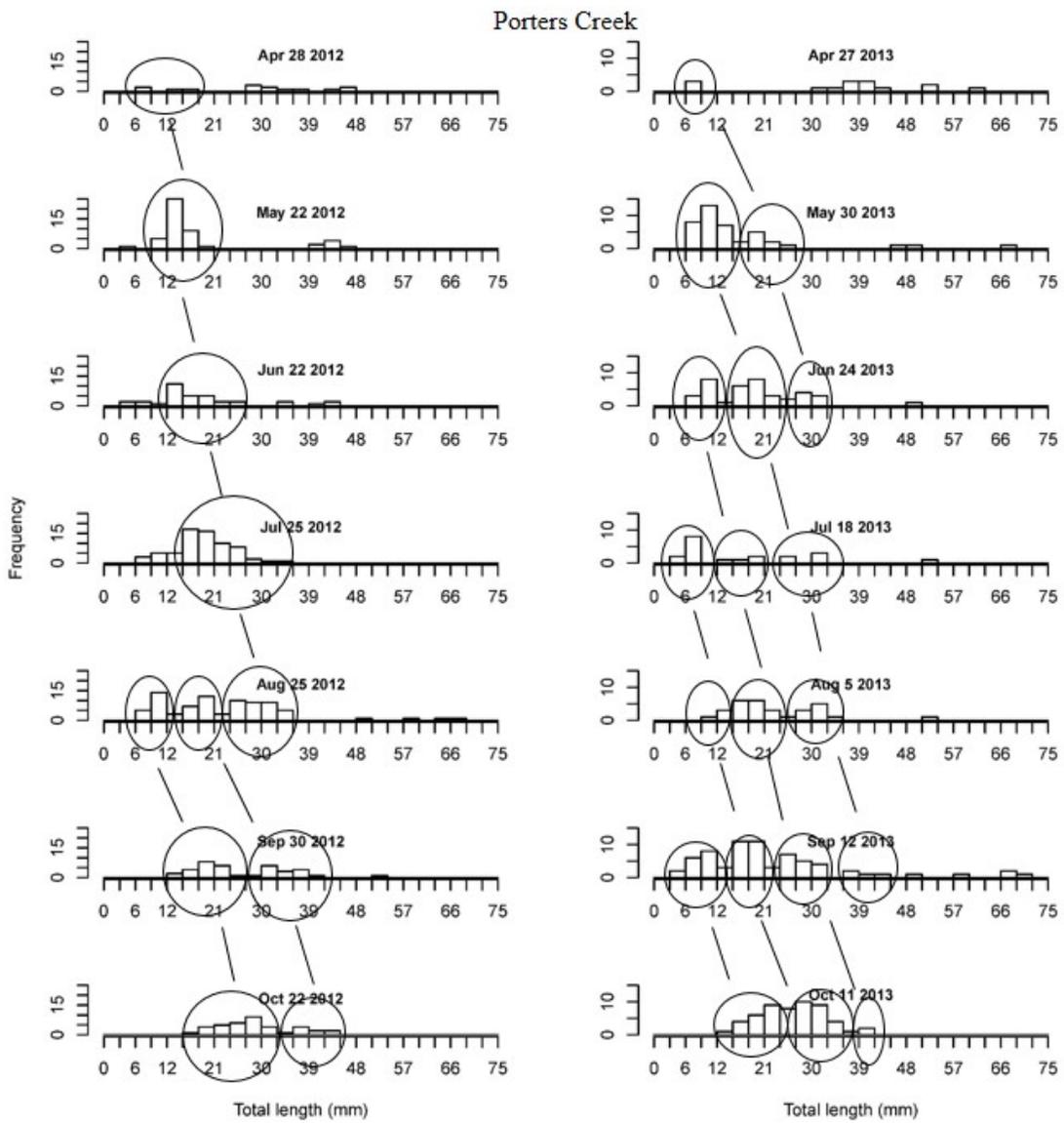


Figure 6.3 (con't)

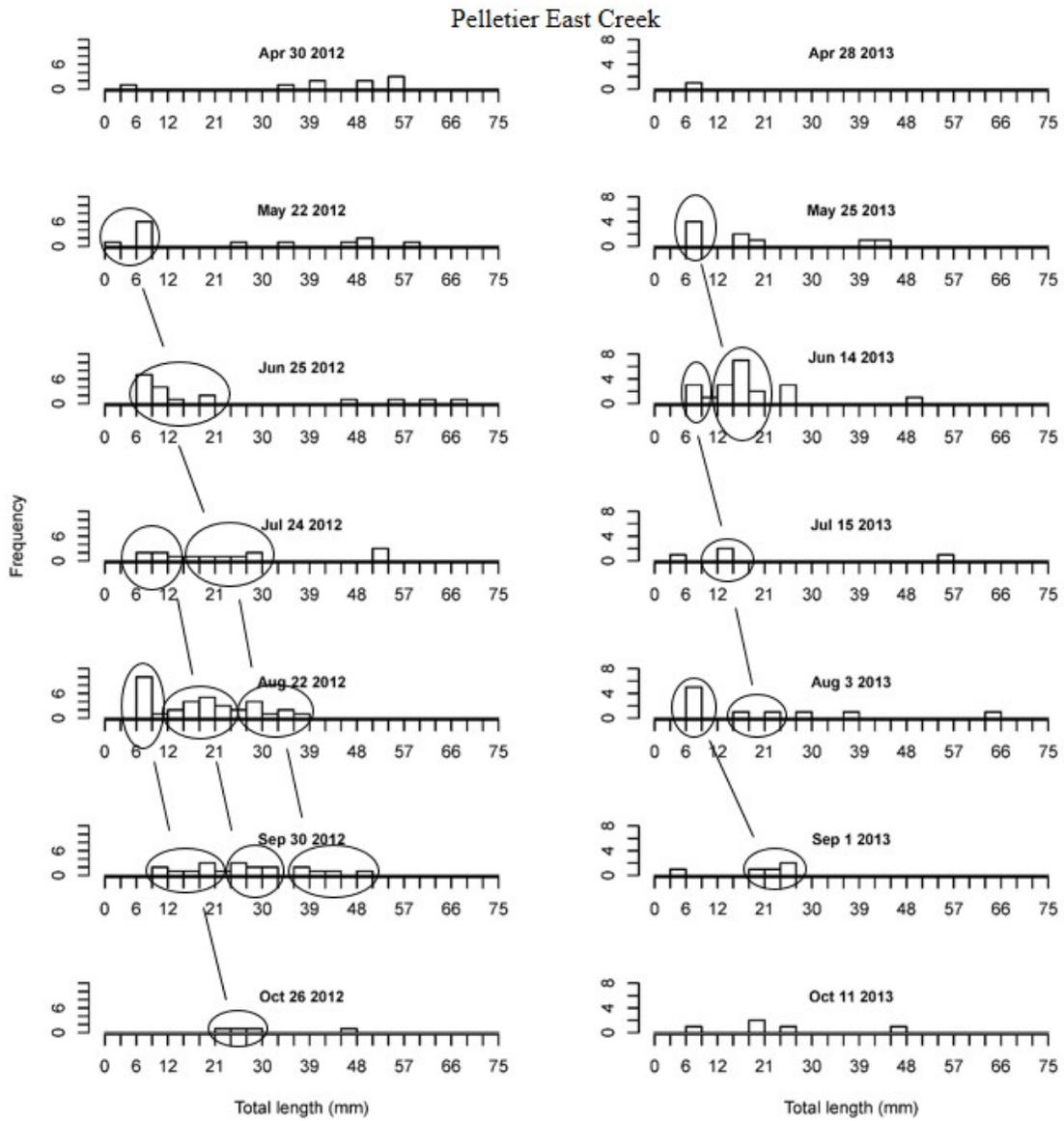


Figure 6.3 (con't)

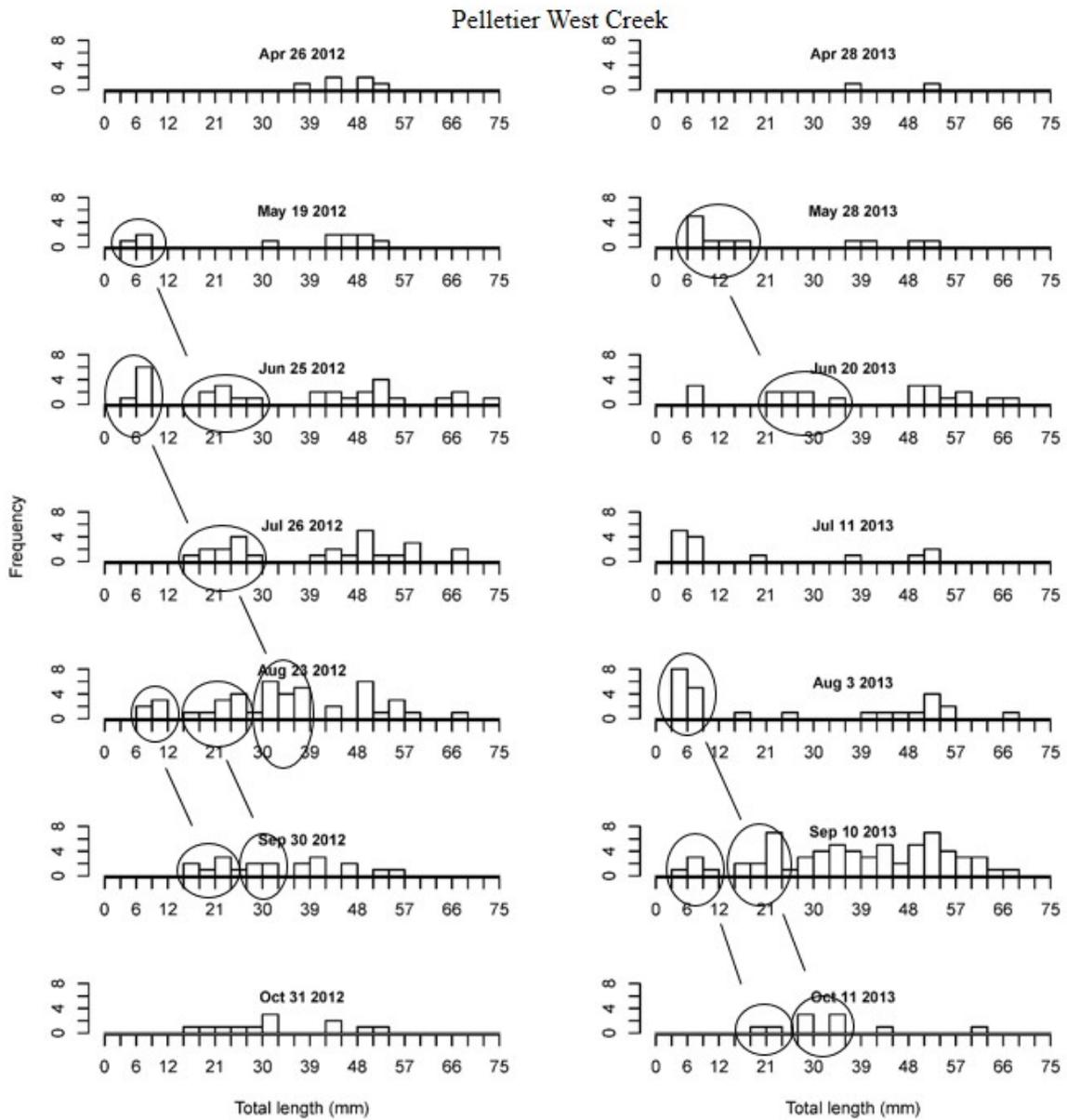


Figure 6.3 (con't)

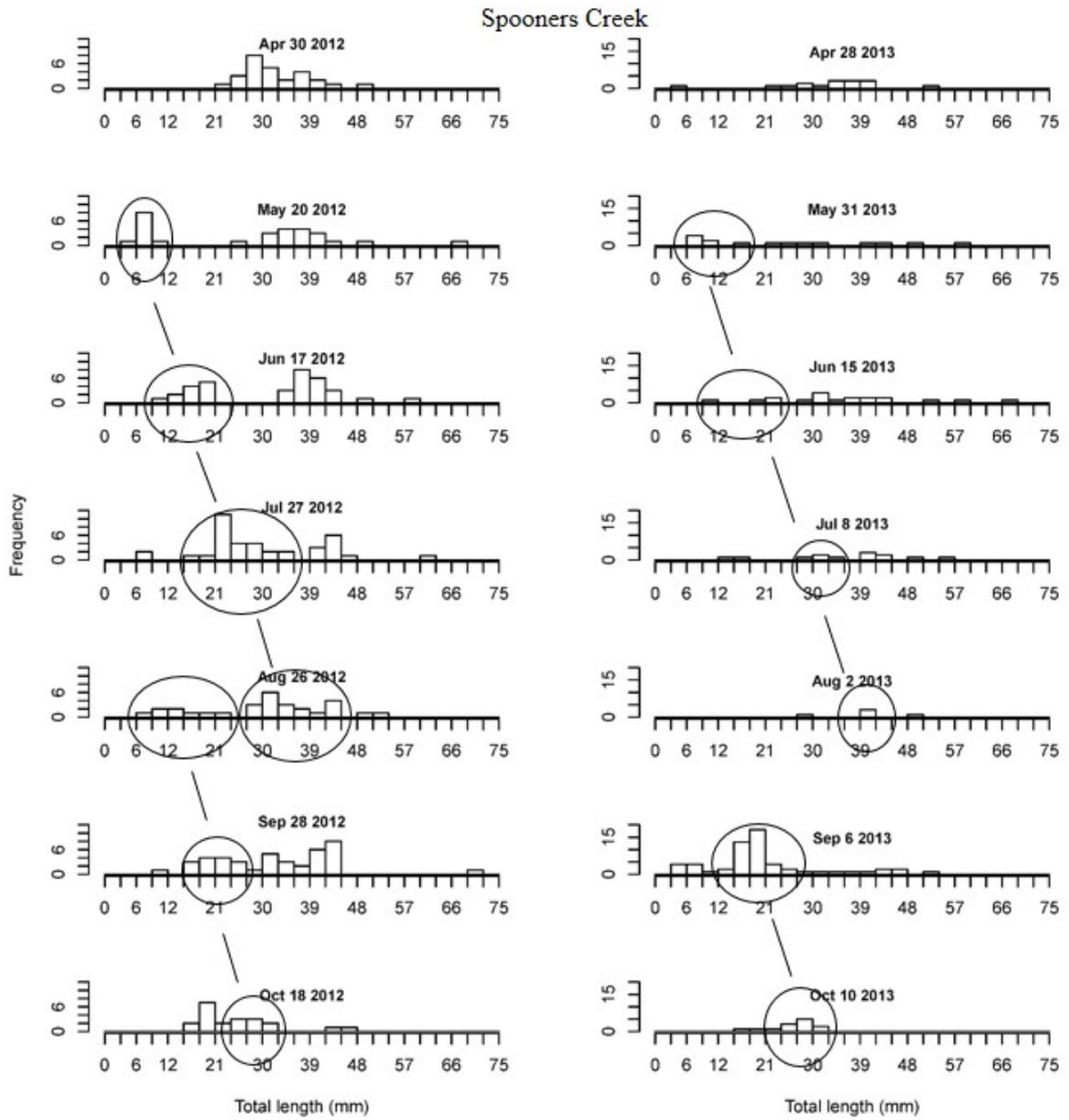


Figure 6.3. (con't)

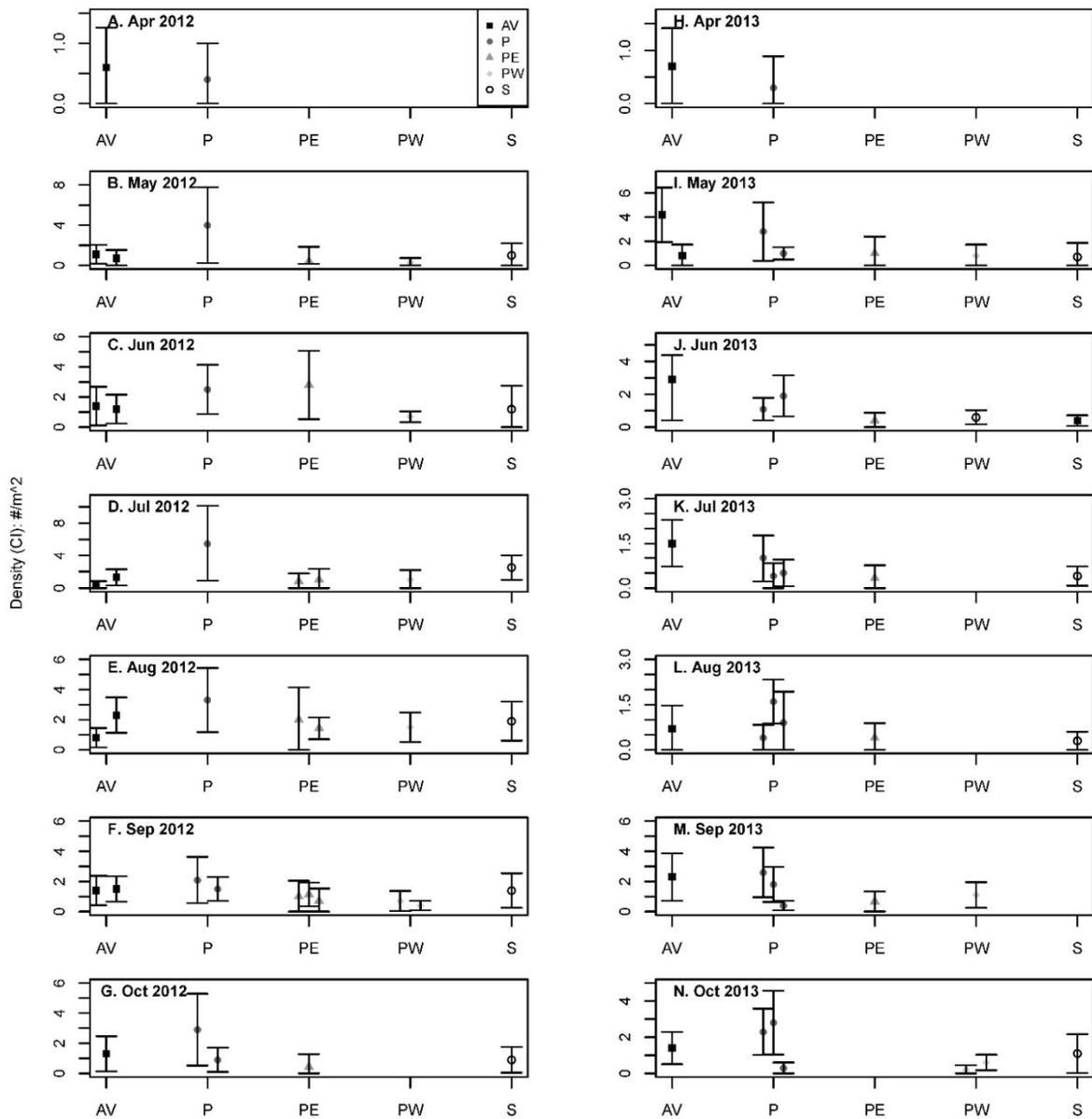


Figure 6.4. Cohort-specific estimates of mean density (\bar{N}) (individuals m^{-2}) (mean \pm confidence interval: CI) (y axis) averaged over the marsh area for seven months and two years of sampling *Fundulus heteroclitus* captured with a 1 m^2 throw trap deployed in the marsh of five tidal creeks (x axis) in coastal North Carolina in 2012 (left column) and 2013 (right column). Different numbers of cohorts were tracked over successive months within- and among creeks; some creeks/months did not have cohorts that were tracked. The x axis is identical among panels; the scale of the y axis differs among panels. Creek abbreviations: AV = Atlantic Veneer, P = Porters, PE = Pelletier East, PW = Pelletier West, S = Spooners. Creek-specific values are jittered around the x axis to avoid overlap for time intervals when more than one cohort was tracked for a creek. The single legend applies to all panels.

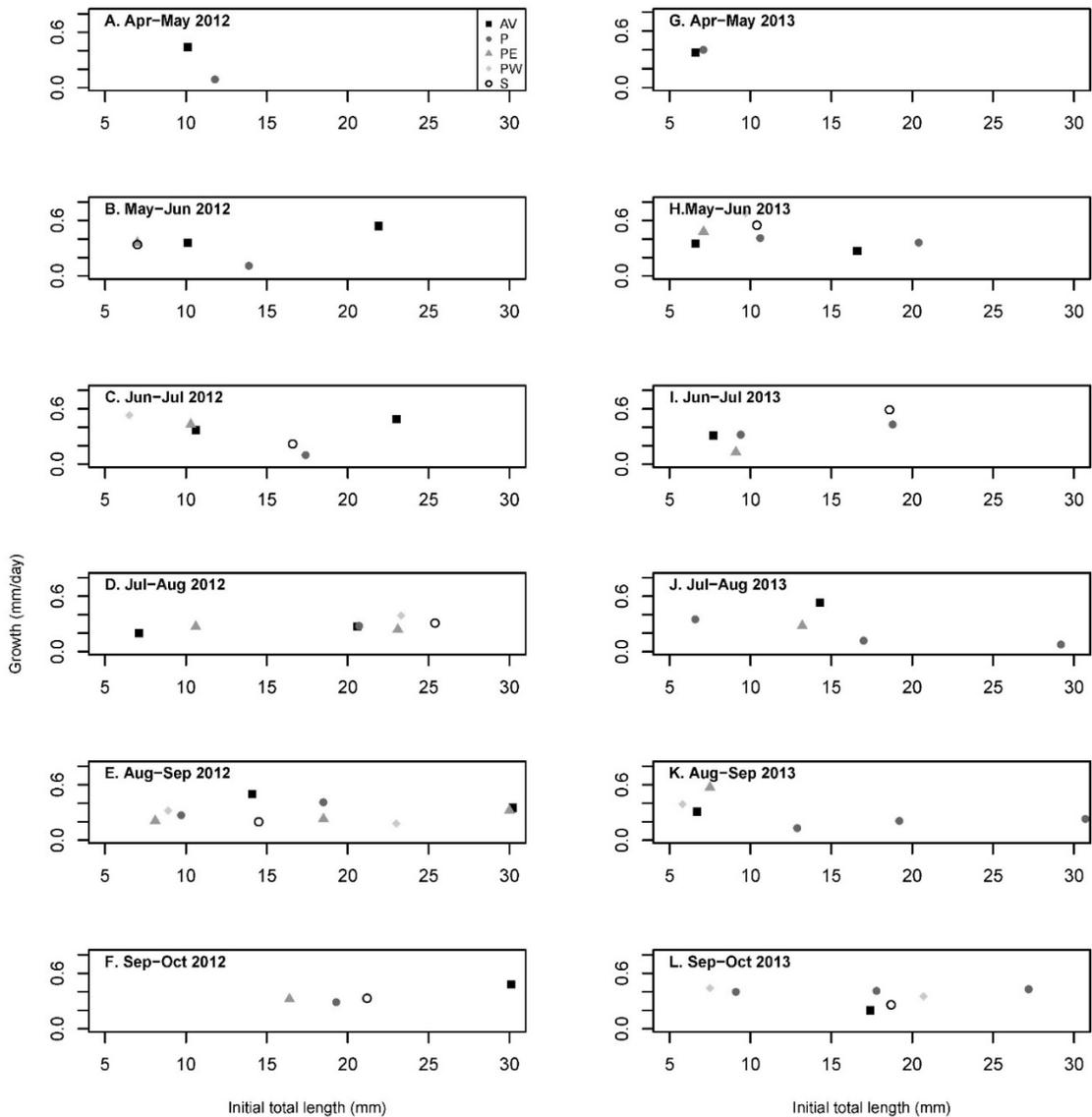


Figure 6.5. Calculations of mean absolute growth rate (mm TL day⁻¹) over six inter-monthly time intervals for *Fundulus heteroclitus* captured with a 1 m² throw trap deployed in the marsh of five tidal creeks in coastal North Carolina in 2012 (left column) and 2013 (right column). The growth rate was calculated as the difference in mean sizes of individuals comprising a cohort between successive months. For each panel fish are separated by initial mean total length at the start of the interval (x axis). Different numbers of cohorts were tracked over successive months within- and among creeks. The scales of both the x and y axes are identical among panels. Creek abbreviations: AV = Atlantic Veneer, P = Porters, PE = Pelletier East, PW = Pelletier West, S = Spooners. The single legend applies to all panels.

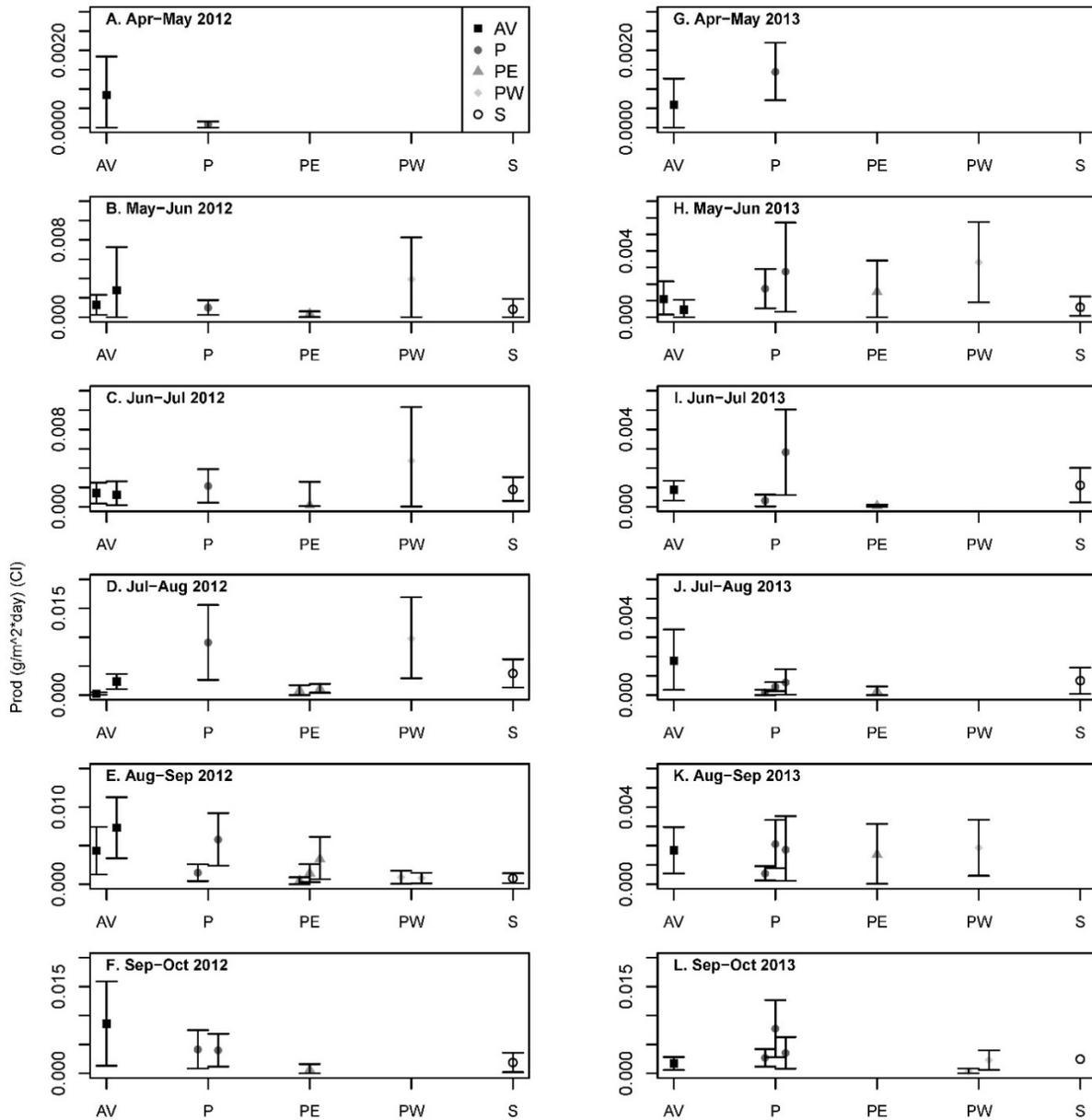


Figure 6.6. Cohort-specific estimates of dry weight production ($\text{g m}^{-2} \text{day}^{-1}$) (mean \pm CI) (y axis) averaged over the creek-wide marsh area for *Fundulus heteroclitus* captured by a 1 m^2 throw trap on the marsh surface in five tidal creeks (x axis) in coastal North Carolina in 2012 (left column) and 2013 (right column). Different numbers of cohorts were tracked over successive months within- and among creeks; some creek/time combinations did not have cohorts that were tracked. The x axis is identical among panels; the scale of the y axis differs among panels. Creek abbreviations: AV = Atlantic Veneer, P = Porters, PE = Pelletier East, PW = Pelletier West, S = Spooners. Creek-specific values are jittered around the x axis to avoid overlap where more than one cohort is tracked for a creek. The single legend applies to all panels.

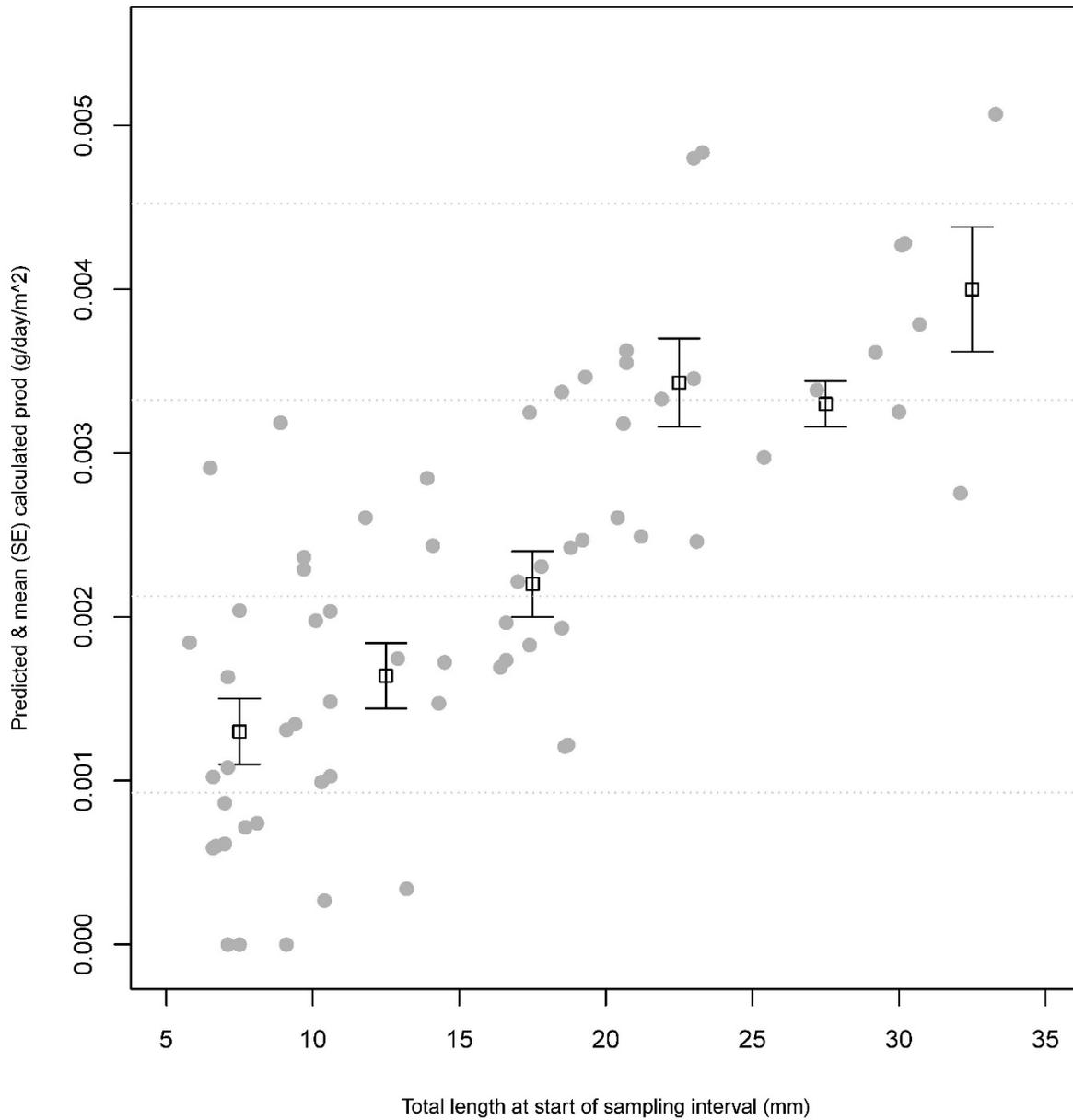


Figure 6.7. Mean (SE) areal dry weight production on the vegetated marsh surface ($\text{g m}^{-2} \text{day}^{-1}$) (open symbols/lines) and predicted production (gray symbols) of *Fundulus heteroclitus* (y axis) in five tidal creeks in coastal North Carolina as a function of mean total length of each cohort tracked for production at the start of each monthly time interval over which production was calculated (x axis). Predictions are from the best-fitting general linear model fitted to production data; this model contained total length as a meaningful covariate of production (2.5 and 97.5 credible intervals not overlapping with zero) (see Table 6.4). Calculated data are binned for each 5 mm increment of total length and centered at the midpoint of each bin.

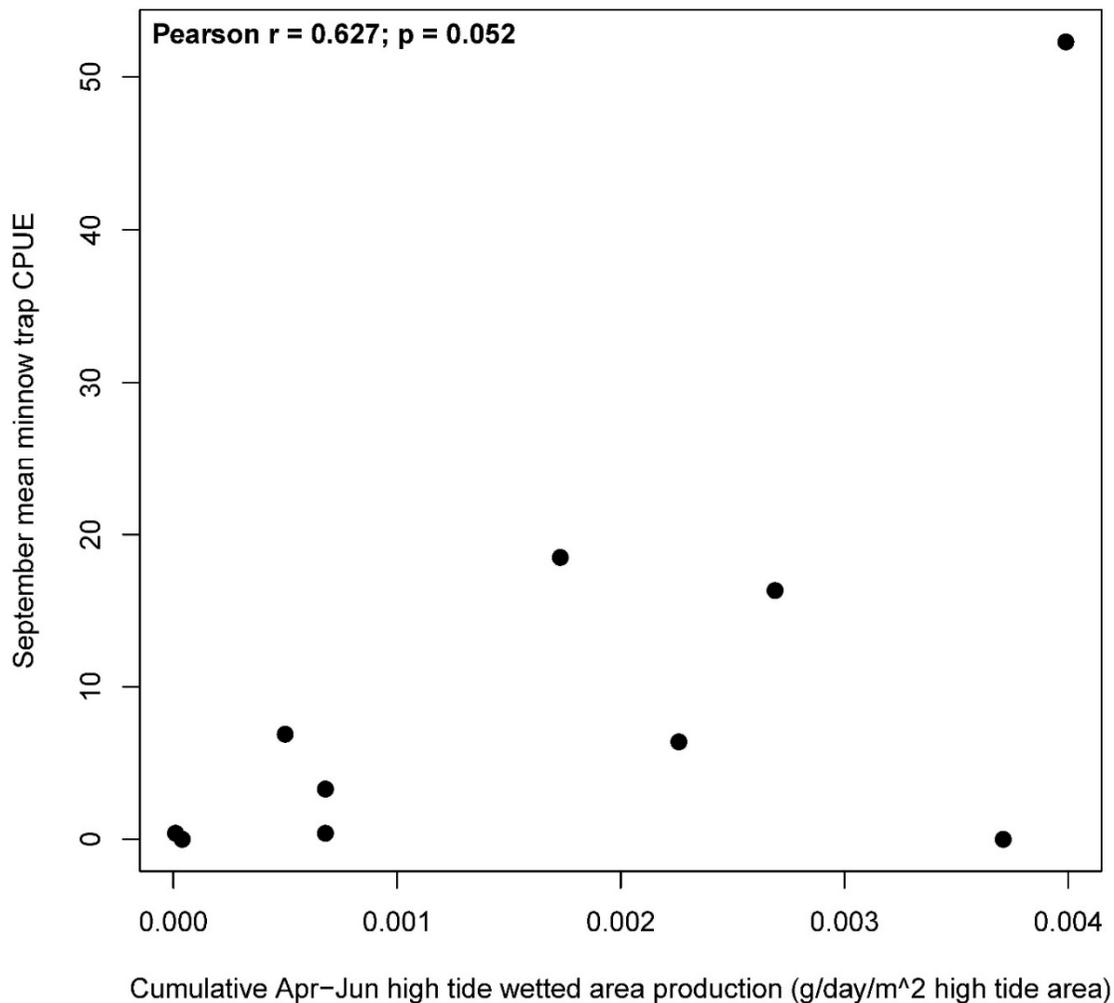


Figure 6.8. Relationship between cumulative springtime age-0 larval/juvenile production and minnow trap catch-per-unit-effort (CPUE) of adult *Fundulus heteroclitus* from five tidal creeks in coastal North Carolina. The x data are values of production summed across all cohorts tracked between April and June for each of five creeks and each of two years (2012 and 2013) and extrapolated to the full high tide wetted area in each respective creek. The y data are mean minnow trap CPUE values from September 2012 and September 2013 in each creek. The value for the correlation coefficient and the p-value for the relationship are provided in the graph panel.

CHAPTER 7. CONCLUSIONS

Salt marshes have long been altered by humans despite the many ecosystem services that they provide (Teal and Howes 2002; Barbier et al. 2011). More than half of the original salt marsh area in the United States has been lost due to development (Kennish 2001). The conservation of these highly imperiled habitats (Kennish 2001; Gedan et al. 2009) requires a more thorough understanding of how these areas and the nekton that use them are affected by anthropogenic encroachment (Peterson and Lowe 2009; Lowe and Peterson 2014).

The state of North Carolina has identified a need for more fishery-independent information to determine the effect of wetland coverage on fish and invertebrate communities and demographics in its estuaries (North Carolina Division of Marine Fisheries 2010; North Carolina Department of Environmental Quality 2016). While recent work has advanced the understanding of landscape-level human impacts on sessile benthic communities as well as nutrient and pathogen loadings in U.S. South Atlantic estuaries, relatively little work has been conducted on examining the impacts of development on nekton communities or nekton population demographics. This research project investigated nekton community structure, fish movement and fish demographics across a gradient of landscape-level habitat and anthropogenic effects in first-order saltwater creeks. It filled gaps in the current knowledge of specific impacts of urbanization in a section of the rapidly developing U.S. South Atlantic coastal zone.

Chapter 2 of this dissertation found that *Fundulus heteroclitus*, a resident species to northwest Atlantic coastal salt marshes, and *Lagodon rhomboides*, a transient species, dominated catches from both the throw trap and minnow trap gears. *Fundulus heteroclitus* was the main species at inherently shallow sites possessing intact marsh mosaics while *Lagodon rhomboides* was the main species at developed sites that exhibited loss of salt marsh, altered shoreline, and

anthropogenically deepened water. Water depth, the presence/absence of a culvert, and the presence/absence of salt marsh immediately downstream were factors important to sample dissimilarities for the throw trap across both years of sampling. Percent marsh in creeks and watershed imperviousness were factors contributing to sample dissimilarities for the minnow trap in both years. The results of this community analysis emphasize the importance of intact marsh mosaics at creek-wide spatial scales and show the effects of changing landforms on nekton communities in saltwater creeks.

Chapter 3 focused on changes to nekton communities at within-creek spatial scales. Despite their close proximity to non-impacted sites, sites that were anthropogenically impacted (loss of marsh, armored shoreline and deepened waters) separated in ordination space from non-impacted sites as well as from reference sites; impacted sites possessed nekton communities dominated by the transient species *Lagodon rhomboides*. The resident species *Fundulus heteroclitus* dominated communities at the reference and non-impacted sites. Batch tagging and recapture of *Fundulus heteroclitus* revealed that this species had a lower probability of moving past crossings to sites possessing common anthropogenic impacts to salt marsh creeks, such as loss of marsh surface and deepened waters from dredging and culvert scour. Current speed past crossings influenced rates of movement but crossing length did not influence movement rates. The results of this chapter have ramifications for the ability of fragmented salt marshes to relay secondary production to higher-level consumers in open-water estuaries downstream (Kneib 2000).

Chapter 4 used individual passive integrated transponder (PIT) tag detection histories to track fine-scale tidally-mediated movement patterns as well as rates of apparent survival of *Fundulus heteroclitus*. PIT tags have not been used to track vital rates of *Fundulus heteroclitus*

before, owing to what historically have been PIT tag sizes too large to implant in small-bodied fishes, the inability of ‘off-the-shelf’ electrical-powered detection gear to re-sight fish in saltwater, and the inherent attenuation of radio frequencies in saltwater (Bogie 1972). In Chapter 4 the physical read ranges of 12.5 mm PIT tags were determined across a range of water depths and tag heights within the frame of vertical custom-made antennas in order to determine physical constraints on PIT tag detection in high salinity waters; 12.5 mm tags are one of the sizes of PIT tags that can be implanted in *Fundulus heteroclitus* without adverse effects (Brewer et al. 2016). Custom-made detection antenna arrays were used to document regular patterns of ingress of tagged *Fundulus heteroclitus* into salt marsh creeks on flood tides and egress on ebb tides. Detection data were also used to estimate rates of apparent survival in a salt marsh creek over a nine-month monitoring period. This study represents one of the few studies of apparent survival of this keystone salt marsh species (Meredith and Lotrich 1979). It expands on the limited body of scientific literature using PIT tags to study the ecology of saltwater fishes (Adams et al. 2006; Meynecke et al. 2008; Hering et al. 2010; Barbour et al. 2014).

Chapter 5 focused on estimating demographics of adult *Fundulus heteroclitus* in North Carolina tidal creeks. Apparent survival was similar among creeks with different levels of watershed imperviousness but densities of adults (> 40 mm total length) was lower in creeks that, due to development, had lost salt marsh from their high tide wetted areas. It also documented fidelity of individual fish to the respective creeks in which they were caught, tagged and released; it can thus be reasonably assumed that estimates of demographic parameters apply to the specific areas of the creeks that were sampled.

Model fitting to multiple landscape-level factors in Chapter 6 showed that areal production of age-0 *Fundulus heteroclitus* on the marsh surface is not diminished by loss of

marsh area in a creek or increasing intensity of watershed development. That areal rates of production on the marsh platform were not substantially reduced in more altered creeks and watersheds should give North Carolina fishery and coastal managers pause; creeks with high marsh percentages but within urbanized watersheds – those generally less protected by the strategic habitat nomination process for this region of North Carolina (Jensen et al. 2014) - are maintaining areal rates of within-marsh production. Ironically, these areas have become incidental sanctuaries for some fish and shellfish species due to a combination of permanent harvest closures as well as perceptions by the public that species still legally harvestable in these creeks are too risky to handle or consume (pers. obs.).

The research presented in Chapter 5 found that higher relative abundances of adult *Fundulus heteroclitus* were associated with creeks with greater percentages of marsh within their high tide wetted areas. Given low rates of immigration from outside areas and similar rates of apparent survival of adults, a possible mechanism for this trend is that higher rates of creek-wide larval/juvenile production translate into subsequent higher abundances of adults in those creeks than others. In Chapter 6 I tested for a correlation between cumulative springtime larval/juvenile production extrapolated to the high tide wetted area in each creek and the mean creek-wide catch-per-unit effort (CPUE: proxy for creek-wide density) of recently recruited adults in September of each of two years. The relationship was positive with a significance value that was marginal. This suggests that higher creek-wide production of immature fish, which are closely linked to vegetated marsh, is a likely mechanism for higher creek-wide abundances of adult fish in tidal creeks with greater percentages of marsh coverage.

Watershed development is viewed as a human ‘cost’ factor compromising nekton production (and components of production) in North Carolina estuaries (Deaton et al. 2006).

The analysis revealed that the nekton community sampled by one gear type was affected by watershed development (Chapter 2); the community changes from dominance by *Fundulus heteroclitus* to dominance by *Lagodon rhomboides* with creek-wide marsh loss, deepened water, shoreline armoring and increased watershed imperviousness. However, it found that survival, abundance and production of a trophically important species, *Fundulus heteroclitus*, was not affected by this cost. These results agree with the findings of Krebs et al. (2014) that composite indicators of human impact, such as watershed imperviousness, are likely to have species-specific rather than community-wide impacts.

Despite an increasing proportion of the U.S. population living in urbanized areas, studies into the impacts of development on nekton inhabiting urbanizing creeks are ‘grossly underrepresented’ compared to those in non-urban creeks and little research has examined the factors influencing fish abundance and composition in urban creeks (Paul and Meyer 2001; Meyer et al. 2005). Additionally, the effects of urbanization on saltwater fishes are little studied despite the fact that habitat destruction is a primary threat to marine ecosystems (Carr et al. 2003; Kappel 2005). And despite increasing human impacts in the U.S. coastal zone, there has been little research into specific anthropogenic factors influencing vital rates of fishes or decapods in saltwater creeks, which contrasts with their freshwater counterparts (Hughes et al. 2014). Further, estimates of biological production of non-salmonid fishes along a ‘gradient of urbanization’ (McDonnell and Pickett 1990) are virtually non-existent for both freshwater fishes (Paul and Meyer 2001) and saltwater fishes (Able 1999). Rapidly developing environments (such as the North Carolina coastline) are important places to research given an expanding human ‘footprint’ in the U.S. South Atlantic coastal zone (Terando et al. 2014) and into salt marsh habitats (Gedan et al. 2009). These facts were motivations for this research program.

This dissertation represents one of the few investigations into the specific anthropogenic impacts on nekton species across a gradient of habitat types and anthropogenic impacts in estuaries. This work extended the recent analyses of estuarine nekton communities along urbanization gradients (Partyka and Peterson 2008; Lowe and Peterson 2014; Krebs et al 2014) by estimating movements and demographics of a dominant nekton species in salt marsh ecosystems. It was conducted in a different region than these other investigations and a different ecosystem than recent work on impacts of urbanization on nekton communities in mangrove ecosystems (Krebs et al 2014).

This study helps address uncertainty into how habitat and anthropogenic factors operating over different scales influence demographics and community composition of fishes and invertebrates in tidal creeks across an urbanizing landscape. Future studies investigating human impacts to tidal creek nekton in this region would contribute to addressing uncertainty about these impacts by working with other species that support valuable commercial and recreational fisheries in the region. For example, *Leiostomus xanthurus* is a commercially and recreationally important offshore-spawned species whose larvae recruit to North Carolina estuaries (and others estuaries in the U.S. South Atlantic) during winter (Warlen and Burke 1990). Individuals use tidal creeks and salt marshes for nursery and growth (Hettler Jr. 1989; Ross 2003) before migrating back to the ocean later in the summer of their first year of life. Similar to this study, it would be informative to estimate demographics of this species and relate those estimates to habitat features as well as anthropogenic factors that the state of North Carolina has identified as ‘costs’ compromising secondary production in its nomination of strategic habitat areas (Jensen et al. 2014). *Callinectes sapidus* is another valuable species for which little demographic information exists on how tidal creek populations of juveniles or adults of this species respond to

typical anthropogenic impacts in these systems; PIT tagging this species along with use of autonomous detection gear offers the potential to more precisely and accurately estimate survival rates than artificially tethering individuals within different habitat types (Hovel and Lipcius 2002).

PIT tagging and associated autonomous detection arrays are powerful tools that help increase precision about estimates of survival of fish populations relative to traditional mark-recapture techniques (Hewitt et al. 2010). However, there is considerable expense and maintenance associated with this gear. Additionally, surgical implantation of PIT tags is a time-consuming process compared to tagging fish with Visible Implanted Elastomer (VIE) batch markings. Future studies into the demographics of *Fundulus heteroclitus* or other small-bodied nekton, such as age-0 *Leiostomus xanthurus*, would be well served to use both tag types. Autonomously resighted PIT tags implanted into a relatively small number of individuals would allow precise estimates of survival (Chapter 3) while batch tagging a large number of individuals with VIE tags would allow more precise estimates of absolute abundance/density relative to using PIT tags as a sole marking device. Ultimately the choice of the tag type(s) for future studies of tidal creek nekton should be guided by the research question, logistics, sample site characteristics, catch rates of the target species, and the body size and tolerance to surgical tag implantation by the focal species.

Information on abundance, growth, survival and production of fishes is invaluable to aid in the preservation and restoration of essential fish habitats (Able 1999; Beck et al. 2001). However, studies into the status and trends of biological production become more difficult the further coastal habitats become altered from baseline conditions (Peterson and Lowe 2009). Given the forecasts of increasing human population growth in the southeastern U.S. coastal zone

(Ternado et al. 2014) and continued conversion of salt marshes to armored shorelines (Lowe and Peterson 2014; Gittman et al. 2015), additional studies into the anthropogenic impact to tidal creek nekton are urgently needed. A greater understanding of the effects of anthropogenic factors will help guide management efforts to both protect and rehabilitate these critical areas.

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APPENDIX A

Supporting information for Chapter 3

Code modified from Kéry (2010) for fitting random-intercept binomially distributed generalized linear mixed models (GLMMs) (logit links) via Bayesian inference to data on movement of adult *Fundulus heteroclitus* past road and reference crossings in North Carolina tidal creeks. GLMMs were run through R software by calling JAGS software. Similar code was used for additional models fitted to other combinations of covariates (see Table 3.3).

```

model {

##### Priors
for (i in 1:n.creeks) {
  alpha[i] ~ dnorm(mu.int, tau.int) #prior for population random intercepts
}

mu.int ~ dnorm(0,0.000001) #hyperprior for grand mean random intercepts
sigma.int ~ dunif(0, 100) # hyperprior for standard deviation of random intercepts
tau.int <- 1 / (sigma.int*sigma.int) #calculated precision for random intercepts

beta1 ~ dnorm(0,0.000001)
beta2 ~ dnorm(0,0.000001)
beta3 ~ dnorm(0,0.000001)
beta4 ~ dnorm(0,0.000001)

##### likelihood
for (i in 1:n.obs) {
  C[i] ~ dbin(p[i], N[i])
  logit(p[i]) <- alpha[CreekCode[i]] + beta1*PercentMarsh[i] + beta2*CurrentVelocity[i]
                + beta3*CurrentVelocitySquared[i]
                + beta4*PercentMarsh[i]*CurrentVelocitySquared[i]

##### Posterior predictive check using a chi-square discrepancy measure
ExpC[i] <- N[i] * p[i]
E[i] <- pow((C[i]-ExpC[i]),2) / (ExpC[i] + 0.5)
C.new[i]~dbin(p[i], N[i]) #Create replicate data set
E.new[i] <- pow((C.new[i]-ExpC[i]),2) / (ExpC[i] + 0.5)

}

fit <- sum(E[]) #sum of squared residuals for actual data set
fit.new <- sum(E.new[]) #sum of squared residuals for new data set
test <- step(fit.new-fit) #Bayesian probability value

} #end model

```

APPENDIX B

Supporting information for Chapter 5

Representative code used to fit a hierarchical formulation of the Cormack Jolly-Seber (CJS) model and an ad-hoc formulation of the Lincoln-Petersen (LP) estimator in a Bayesian framework and used to estimate rates of apparent survival (Φ), tags at risk, detection probability (p) (via the CJS model) and monthly abundance (\hat{N}_t) (via the LP estimator) of *Fundulus heteroclitus* in tidal creeks in coastal North Carolina.

```

model {
##### Section 1 LP ad-hoc
for (a in 1:6) {
    FractionTagged[a] ~ dunif(0,1) # prior for fraction tagged in monthly (a) recap sample
}

##### Section 2 CJS priors
mean.S ~ dunif(0,1) # uninformative prior for  $\Phi$  on probability scale
mu_S <- log(mean.S/(1-mean.S)) # logit transformation
mean.p ~ dunif(0,1) # uninformative prior for  $p$  on probability scale
mu_p <- log(mean.p/(1-mean.p)) #logit transformation

for (i in 1:4) { # this model run has two partial regression coefficients for  $\Phi$  and  $p$ , respectively
    b[i] ~ dnorm(0,1.0E-6) # priors for intercepts and slopes of logistic models for  $\Phi$  and  $p$ 
}

for (i in 1:nind) {
    p[i,1] ~ dbern(1) # tagging occurs at time 1 so p[1] not estimated
}

##### Section 3 CJS logistic models for  $\Phi$  and  $p$ 
for(i in 1:nind) {
    for(j in 1:nocc-1) {
        logit(phi[i,j]) <- mu_S + b[1]*tagtype[i] + b[2]*(temp[j]-AveTemp)
    }
    for(j in 2:nocc) {
        logit(p[i,j]) <- mu_p + b[3]*tagtype[i] + b[4]*(temp[j]-AveTemp)
    }
}

##### Section 4 CJS calculated values
AveTemp <- mean(temp[]) # covariate centering

for (j in 1:nocc-1) {
    AvePhi[j] <- mean(phi[1:nind,j]) #average  $\Phi$  across individuals by occ
}

for (j in 1:AdjPhiEsts) {

```

```

for (i in 1:nind) {
  daily_phi[i, j] <- pow(phi[i, PhiIndex[j]], 1/days[j]) # adjustment for some occasions >24 h
}
}

for (j in 1:AdjPhiEsts) {
  Ave_daily_phi[j] <- mean(daily_phi[,j])
}

phi_over_season<-prod(AvePhi[1:PhiEsts])
Daily_phi_over_season<-mean(Ave_daily_phi[])

for (j in 1:nocc) { #was (j in 2:nocc) {
  AvePSmallTag[j] <- mean(p[1:65,j]) # average p across small tags by occasion
}
}
AveP_Over_SeasonSmallTag <- mean(AvePSmallTag[2:nocc]) # average p across season

for (j in 1:nocc) { #was (j in 2:nocc) {
  AvePLargeTag[j] <- mean(p[66:149,j]) # average p across large tags by occasion
}
}
AveP_Over_SeasonLargeTag <- mean(AvePLargeTag[2:nocc]) # average p across season

##### Section 5 LP ad-hoc abundance
for (a in 1:1) # first month of season
{
  MonthlyPhi[a] <- prod(Ave_daily_phi[startDay[a]:endDay[a]])
  TagsAtRisk[a] <- NumTagged*MonthlyPhi[a]
  mTags[a] ~ dbin(FractionTagged[a], nTags[a])
  N_hat[a] <- TagsAtRisk[a]/FractionTagged[a]
  Density[a] <- N_hat[a]/Area
}
for (a in 2:6) # subsequent months
{
  MonthlyPhi[a] <- prod(Ave_daily_phi[startDay[a]:endDay[a]])
  TagsAtRisk[a] <- TagsAtRisk[a-1]*MonthlyPhi[a] +
  newReleases[a]*MonthlyPhi[a]*FractionMonth[a]
  mTags[a] ~ dbin(FractionTagged[a], nTags[a])
  N_hat[a] <- TagsAtRisk[a]/FractionTagged[a]
  Density[a] <- N_hat[a]/Area
}

##### Section 6 Likelihood
for(i in 1:nind){
  z[i,first[i]]~dbern(1)
  for(j in (first[i]+1):last[i]){
    mu1[i,j]<-phi[i,j-1]*z[i,j-1]
  }
}

```

```
    z[i,j]~dbern(mu1[i,j])
    mu2[i,j]<-p[i,j]*z[i,j]
    x[i,j]~dbern(mu2[i,j])
  }
}
} # end model
```